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Age-age correlations, trait correlations, and wood property variation for an Alnus glutinosa (L.) Gaertn provenance study

Terry Lean Robison
Iowa State University

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AGE-AGE CORRELATIONS, TRAIT CORRELATIONS, AND WOOD PROPERTY VARIATION FOR AN ALNUS GLUTINOSA (L.) GAERTN. PROVENANCE STUDY

Iowa State University PH.D. 1984

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Age-age correlations, trait correlations, and wood property variation for an *Alnus glutinosa* (L.) Gaertn. provenance study

by

Terry Lean Robison

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of the
Requirements for the Degree of
DOCTOR OF PHILOSOPHY

Department: Forestry
Major: Forestry (Forest Biology-Wood Science)

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For the Major Department

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For the Graduate College

Iowa State University
Ames, Iowa

1984

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GENERAL INTRODUCTION

Explanation of Dissertation Format

This dissertation is presented in the alternate format style that was approved by the Graduate Faculty of Iowa State University on May 25, 1979. The format consists of a general introduction followed by individual papers that have been prepared for submittal to scholarly journals. These are followed by an overall summary and discussion section that serves to unite the individual papers.

Two papers that deal with research on European black alder are presented in this dissertation. Both are the results of ongoing research initiated by the junior author on both papers, Dr. Richard B. Hall. He had initiated the collection of the trees to be used to determine juvenile-mature correlations for growth properties. I assumed control of the project after the collection, established the sampling and measurement schemes to be used to collect data, and determined that wood quality should be assessed because these trees were of known geographic background.

Scope of Study

Juvenile-mature correlations for height, diameter, and volume for Alnus glutinosa (L.) Gaertn. were determined using stem-analysis data. Through rigorous sampling of the trees involved, it also was possible to develop juvenile-mature correlations for the wood quality traits as well. The information gathered will be useful for making recommendations on when selection can take place for these traits.

Additionally, provenance variation in specific gravity and fiber length was determined. Unlike previous wood quality studies, the material in this study was source-identified. Finally, trait correlations were calculated to determine how selection for one of the traits studied would influence the other traits.

Collection of Study Materials

The trees used in these studies were collected from an Alnus glutinosa provenance test located on a graded mine spoil in Muskingum County in southeastern Ohio (Funk 1979). The surface was rocky and generally level with a pH between 4.0 and 5.0 at the time of planting (Funk 1973; Miller 1983). One-year-old seedlings were bar-planted in April 1963, in a randomized complete block design at 2.1 m square spacing with 3 replications X 15 provenances X 25 trees/provenance/plot. The 15 sources were collected from the central part of the species' range with most being of German origin. Observations in June 1979 indicated that survival was good, but the amount of flowering was low considering the age of the plantation and European black alder's known precocity (Miller 1983).

In November 1978, a total of 42 trees representing 14 of the original 15 provenances were harvested. The poorest performing provenance in the original study was omitted (source 19- Uppland Sweden). Three trees were taken from each provenance in each replication. The trees were randomly selected from dominant and co-dominant trees on the interior of the plots ignoring those with

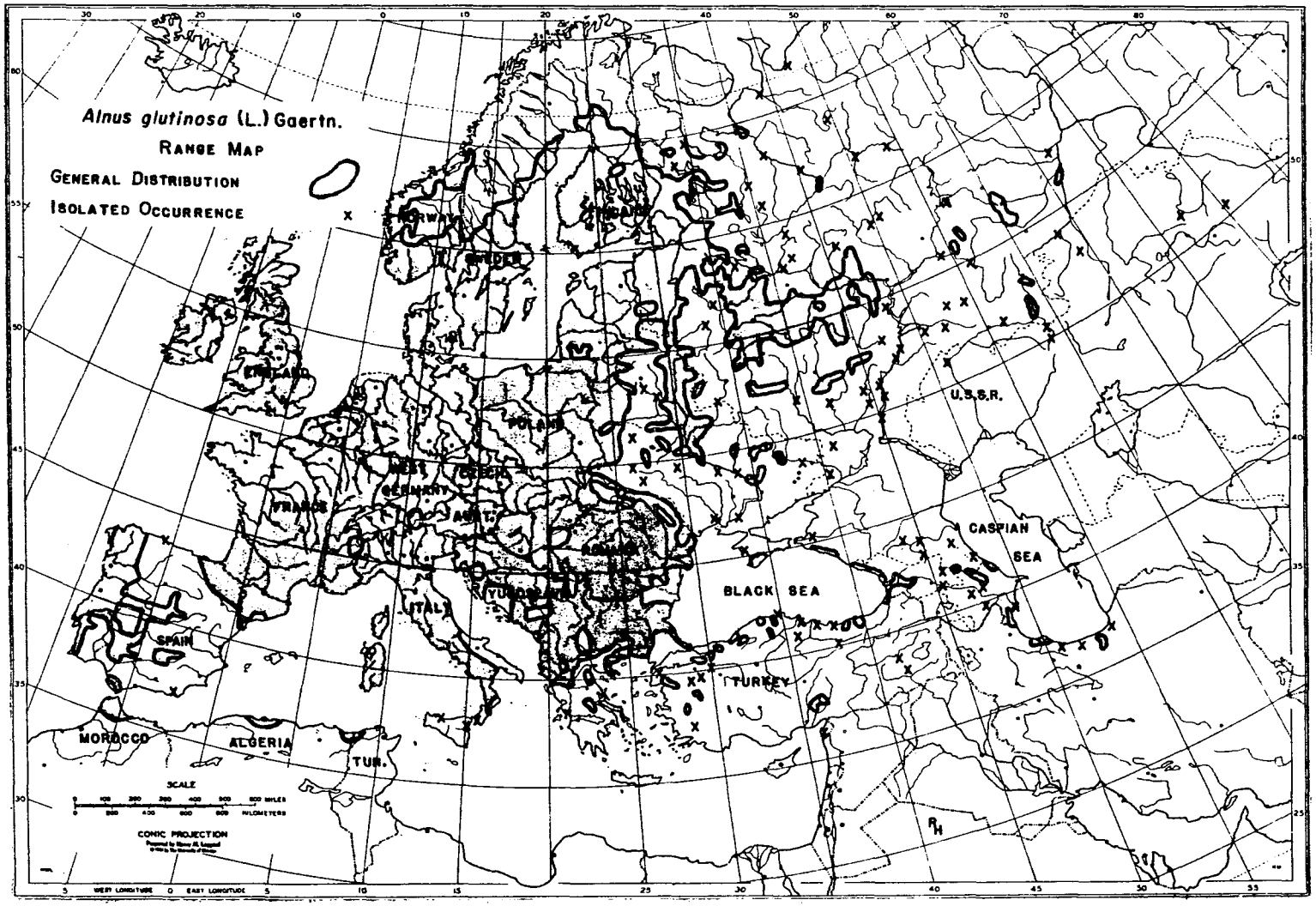
serious defects. The trees were trucked to Iowa State University, Ames, Iowa for the analysis described herein.

Background

The genus Alnus has received considerable attention for some time as a possible component in intensive culture plantations (Dickman 1975; Gordon and Dawson 1979; Zavitkovski et al. 1979; Resch 1979; DeBell and Radwin 1979). This is mainly because of the alder's rapid growth and symbiotic nitrogen-fixing traits. Alders can be used in pure plantations or in mixtures with other species (DeBell and Radwin 1979; Harrington et al. 1979; Plass 1977; Wittmer and Immel 1977) to produce biomass suitable for solid wood, composites, and pulp. Additionally, the U. S. Department of Energy and the International Energy Agency have placed alders high on the priority list of woody species being considered in biomass for energy plantations.

Alnus glutinosa (European black alder) is one species of alder being considered for use in the eastern United States because there are no tree-form alders native to this region (Hall et al. 1983). The natural range of A. glutinosa covers most of Europe, northern Africa, and eastern Asia (Figure 1). Although the species prefers moist sites, its habitat ranges from swampy bottomlands to drier sites up to 1800 m in elevation (Funk 1965). The species grows as a small, multiple-stemmed shrub, or as a somewhat large, single-stemmed tree sometimes reaching over 30 m in height. This wide habitat tolerance and phenotypic variation ensures adequate genetic variation providing an

Figure 1. Natural range of Alnus glutinosa. (Adapted from Robison et al. 1979)


Alnus glutinosa (L.) Gaertn.
RANGE MAP
GENERAL DISTRIBUTION
ISOLATED OCCURRENCE
NORWAY
SWEDEN
FINLAND
U.S.S.R.
POLAND
WEST GERMANY
FRANCE
AUST.
ROMANIA
YUGOSLAVIA
ITALY
BLACK SEA
CASPIAN SEA
SPAIN
TURKEY
MOROCCO
ALGERIA
TUN.
SCALE
CONIC PROJECTION
WEST LONGITUDE
EAST LONGITUDE

excellent opportunity for an introduction and genetic improvement program (Robison et al. 1979; Hall and Maynard 1979; Robison and Hall 1981; Hall et al. 1983).

The first screening of A. glutinosa seed sources in this country began with a provenance test established on a strip-mine in Ohio in 1963 (Funk 1973, 1979). Subsequent provenance tests have been established throughout the eastern U. S. to identify sources adapted to particular regions and sites in this country (Hall et al. 1983; Robison et al. 1979; Hall and Maynard 1979). Based on 16-year data, seed sources from southeastern Germany outperform other sources from central Europe in Ohio (Funk 1979). Four-year data indicate that sources from the Netherlands, Hungary, and northern Germany perform best in central Iowa while sources from Poland and the Baltic States are better adapted to northern Wisconsin conditions (Hall et al. 1983). An unknown source from an Illinois plantation and several sources from Romania have shown the best growth in several plantations in three southeastern states after 4 years (Kellison and White 1979).

Wood Quality Implications

The proportion of young trees used in the forest products industry that are derived from fast grown plantations is increasing and will continue to do so until this source of material provides the majority of furnish in the next 20 years (Zobel 1981). Short-rotation intensive culture (SRIC) forestry will provide a source of much of this material. This will require the selection of sources and individual trees that are

adapted to SRIC environments and have fast growth rates. This allows rapid site establishment and volume production. Often, too much emphasis is placed on this "rate of growth syndrome" (Zobel and Kellison 1978). The production of wood volume is and will remain the major component of wood value (Kellogg 1982), but wood quality traits must be included in determining plus trees so that the wood produced quickly is also usable (Zobel and Kellison 1978).

It is a consensus opinion that wood produced from SRIC plantations will contain a high proportion of juvenile wood (Crist 1983; Zobel 1981; Bendtsen 1978; Einspahr 1976; Jett and Zobel 1975). In both hardwoods and conifers, this causes a reduction in specific gravity and fiber length while increasing fibril angle, moisture content, and reaction wood. These changes usually are deleterious to the properties of conventional forest products.

Because abundant variation exists within species, it should be possible to improve upon juvenile wood properties. Additionally, it should be possible to increase the uniformity between trees by selecting for wood quality (Zobel et al. 1983). Uniform wood is advantageous because it gives a better quality product with greater manufacturing efficiency.

Many times it is assumed that any wood produced from trees can be made usable through advances in forest products technology. This is not always the case. Examples exist of trees having good form and growth rate, but producing undesirable or unusable wood because of low specific

gravity (e.g., Zobel and Kellison 1978). When this wood can be processed, it is usually done at the expense of increased energy usage, reduced yield, or loss in quality (Kellogg 1982). By including wood quality in improvement programs, it should be possible to optimize juvenile wood characteristics while producing a more uniform product as well. It is important for all tree breeding programs to consider wood quality improvement in their objectives, and most important for beginning programs to include from the start.

Early Selection Implications

Identification of superior sources can follow one of two alternatives: 1) wait until the trees of interest reach the desired rotation age and then make selections, or 2) make selections at some fraction of the rotation age hoping that these "early" selections will prove to be superior at the utilization age. Waiting the full rotation length to make selections causes considerable problems especially in long-lived organisms such as forest trees. The long evaluation period is expensive in terms of land area used, time invested by the researcher, lengthened breeding cycles, and the actual costs of overhead, maintenance, and data collection that must be subjected to compound interest. Early selection allows breeders to shorten breeding cycles, reduce expenses, and, most importantly, maximize genetic gain per unit time. These advantages hold provided that there is a good correlation for the trait between the early selection age and the utilization age.

Early selection is a form of indirect selection where selection for one trait is used to improve another trait. Using indirect selection, it is possible to achieve more rapid gains because of the correlated response of the two traits (Falconer 1960). With early selection the selected trait is some characteristic at a young age, and the trait targeted for improvement is the same characteristic at maturity (rotation age). The correlation between a trait at two ages has been referred to as a juvenile-mature correlation, or, in more general terms, as an age-age correlation. The efficiency of early selection is directly dependent on the magnitude of this age-age correlation (Lambeth 1980).

The use of early selection in forestry was pioneered by Schmidt is his work with Scots pine (Nanson 1968; Sziklai 1974). Since then the value of early tests in forestry has been universally accepted, but their efficiency in actual situations has left doubt to their worth (Schmidt 1963; Nanson 1968). In his 1968 doctoral dissertation, Alphonse Nanson reviewed the previous work on early tests in forestry, and subsequently developed a theory on the value of early tests in forest tree selection. He concluded that, by using the concept of correlated genotypic gain, early selection on specific characteristics could yield gains 2 to 3 times greater than those achieved following direct late selection.

The model for early selection is based on the equation for correlated response (Falconer 1960), and has been developed extensively

by Nanson (1967, 1968, 1970, 1974, 1976) and others (Franklin 1977; Squillace and Gansel 1974; Lambeth 1980). The response (or genotypic gain) by directly selecting for a mature characteristic is (Falconer 1960, p. 193):

$$R_m = i_m h_m^2 \sigma_{Pm} \qquad (1)$$

and the correlated response (or correlated genotypic gain (Nanson 1970)) on the mature characteristic by selecting for the same characteristic at a juvenile stage is (Falconer 1960, p. 318):

$$CR_m = i_j h_j h_m r_{Gjm} \sigma_{Pm} \qquad (2)$$

where:

i_m=selection intensity on mature trait

i_j=selection intensity on juvenile trait

h_m^2=heritability for mature trait

h_m=square root of heritability for mature trait

h_j=square root of heritability for juvenile trait

σ_{Pm}=phenotypic standard deviation for mature trait

r_{Gjm}=genetic correlation between juvenile and mature traits.

This equation requires estimates of heritabilities and genetic correlations for a trait at juvenile and mature stages. Because many old studies were designed poorly and lacked replication this information is often unavailable. Additionally, it also would be useful to predict

gain for species that do not have heritability or genetic correlation estimates. To remedy this, the genetic correlation can be put in terms of the phenotypic correlation according to the following equation (Falconer 1960, p. 315):

$$r_{P_{jm}}=h_j h_m r_{G_{jm}}+e_j e_m r_{E_{jm}} \qquad (3)$$

where:

$r_{P_{jm}}$=phenotypic correlation between juvenile and mature traits

e_j=square root of the environmental interclass correlation for juvenile trait

e_m=square root of the environmental interclass correlation for mature trait

$r_{E_{jm}}$=environmental correlation between juvenile and mature traits

h_j, h_m, $r_{G_{jm}}$ as defined previously.

Then, by substitution, the correlated response formula becomes

$$CR_m=i_j(r_{P_{jm}}-e_j e_m r_{E_{jm}})\sigma_{P_m}. \qquad (4)$$

Then, by assuming that $e_j e_m r_{E_{jm}}=0$ the correlated response equation reduces to (Nanson 1968, 1970, 1976):

$$CR_m=i_j r_{P_{jm}}\sigma_{P_m}. \qquad (5)$$

This assumption is based on well designed, replicated studies where it appears that r_E can be held at very low levels. However, recent studies have stated that this assumption may not hold all of the time (Franklin 1977; Lambeth 1980; Namkoong et al. 1972; Namkoong and Conkle 1976). This is because environmental effects, especially the timing of these effects during development, are not accounted for (Franklin 1977). The genetic and environmental components affecting a given trait apparently change in magnitude through the different stages of tree growth (Namkoong et al. 1972; Namkoong and Conkle 1976). Therefore, equation (4) should be used only when rough estimates of CR_m are needed such as when heritability and genetic correlation data are lacking.

Although estimates of CR_m are important, it probably is more important to know whether early selection is more advantageous than late selection, and at what age early selection is the most efficient. By making a few realistic and conservative assumptions, this can be done without heritability and genetic correlation estimates.

The merit of early selection compared to late selection is the ratio of equation (2) to (1), which reduces to (Franklin 1977):

$$CR_m/R_m=(i_j h_j r_{Gjm})/(i_m h_m). \qquad (6)$$

To determine at what age the best relative gain is achieved, the efficiency of early selection (E) is calculated in terms of gain per

year compared to selection at maturity (Squillace and Gansel 1974; Lambeth 1980):

$$E=((i_j h_j r_{Gjm})/(i_m h_m))\cdot(T_m/T_j) \qquad (7)$$

where:

T_m=years to complete a breeding cycle for selection at mature stage

T_j=years to complete a breeding cycle for selection at juvenile stage.

Equation (7) allows different early selection ages to be compared on a gain per year basis. This shows that the efficiency of early selection compared to late selection is determined by the ratio of the selection intensities, the ratio of the square roots of the heritabilities, the genetic juvenile-mature correlation, and the ratio of the years to complete the breeding cycles.

First assume that $i_j=i_m$ (Lambeth 1980). Usually, the selection intensity for an early test can be much higher than the selection intensity at maturity because more individual trees can be tested because of their smaller size (Nanson 1968; Franklin 1977; Kung 1975). Therefore, this is a conservative assumption in that, if $i_j>i_m$, the assumption allows for an overestimate of selection age rather than underestimating it. Underestimation leads to a higher probablility of

including undesirable genotypes or deleting good ones.

Second, assume that $h_j=h_m$ (Squillace and Gansel 1974; Lambeth 1980). It is probable that juvenile heritabilties are greater than the mature heritabilities. This is because test sizes can be kept compact in early tests because the trees are smaller. This reduces environmental and error variances providing conditions to optimize juvenile heritabilities. Again, this is a conservative assumption causing an overestimate of optimum rotation age in most cases.

Finally, assume that $r_{P_{jm}}=r_{G_{jm}}$ (Lambeth 1980). One major drawback to this assumption is that phenotypic correlations are composed of environmental and genetic components. The environmental and genetic correlations can be different in magnitude as well as sign (Falconer 1960). Therefore, it is possible to obtain a positive phenotypic correlation when the genetic correlation is negative. Because the genetic correlation along with the heritability is the actual indicator of the value of an early test (Nanson 1976), it still is possible to make severe mistakes using the phenotypic correlation when r_E is not close to zero. However, in most forest tree early selection experiments, the genetic correlations are as large or larger than their phenotypic counterparts (Lambeth 1980; Steinhoff 1974; Mohn and Randall 1971). Phenotypic correlations therefore provide conservative estimates of the optimum early selection age (Lambeth 1980).

Using these assumptions, the final equation to estimate early selection efficiency is

$$E=rP_{jm}(T_m/T_j). \qquad (8)$$

The selection age optimizing E will be the age yielding the most gain per year (Squillace and Gansel 1974).

SECTION I. JUVENILE-MATURE CORRELATIONS FOR AN *ALNUS GLUTINOSA* (L.) GAERTN. PROVENANCE STUDY

INTRODUCTION

Initial improvement efforts for European black alder (Alnus glutinosa (L.) Gaertn.) have concentrated on provenance testing to determine the variability of important traits and to identify sources adapted to specific geographical regions and sites. The surest method of evaluating these trees would be to observe them periodically through the desired rotation age, and then select those provenances and individuals with desirable traits. However, to avoid the costs of long evaluation periods and shorten breeding cycles, selections should be made as early as possible.

Early selection is a form of indirect selection (Falconer 1960) in which the selected characteristic is a property at an early age and the target characteristic is the same property at a later or utilization age. If the trait of interest is well-correlated at early and later stages, then genetic gain can be greater using early selection rather than waiting the full rotation length to make selections (Falconer 1960; Nanson 1968, 1970; Squillace and Gansel 1974; Kung 1975; Franklin 1977; Rehfeldt 1983).

Provenance tests of European black alder have been established throughout the eastern half of the United States (Robison and Hall 1981). Most of these are 5-years-old or less and cannot be evaluated for longer rotations. The present study utilized 17-year-old trees from the oldest European black alder provenance test in this country (Funk 1973, 1979) to develop juvenile-mature correlations (age-age

correlations) for some growth and wood properties. Direct comparisons between the data collected in this study and other provenance tests should be made with caution, because of likely genotype x environment interactions. This study is intended to give an initial approximation of age-age correlations and only should be used as a guide for selection in the younger provenance tests where correlations are not available. In addition to the age-age correlations, trait correlations are presented to indicate how selection for one particular trait will affect the response of the other traits studied.

MATERIALS AND METHODS

Trees were collected in 1978 from a provenance test in southeastern Ohio (Funk 1973, 1979). The provenance test was arranged in a randomized complete block design with 3 replications. Fourteen of the original 15 provenances were selected for this study with the poorest performing provenance being omitted. One tree was harvested from each provenance in each block yielding a total of 42 trees.

Stem analysis was used to determine past growth characteristics as was done in a similar study with black walnut (Kung 1975). Disks were cut from the trees at heights of 0.3, 0.8, 1.3, 1.8, and 2.5 m and at 1 m intervals thereafter. The lower surface of each disk was sanded, and the distance from the pith to each ring measured to the nearest 0.1 mm along north and west radii. The line of measurement was shifted if branch traces interfered with measurement. Annual heights were estimated to fall between disks where a decrease in ring number occurred. Using the radius and height data, volumes were estimated by a Fortran computer program that calculated the shape of successive 3-disk intervals along a particular growth ring in a tree, and then selected a formula for volume based on this shape from equations for conoid, neiloid, and paraboliod shapes. These interval volumes then were summed to give the total volume at a particular age.

Average whole-tree specific gravity and fiber length were estimated for ages 5, 7, 9, 11, 14, and 17. One provenance was omitted from this part of the study because of deterioration of the disks prior to

analysis. A full discussion of the sampling system used to determine specific gravity and fiber length, and the variation in these properties, can be found in Robison (1984).

Correlations were calculated between juvenile and mature values for volume, height, DBH, specific gravity, and fiber length (referred to as JMVOL, JMHT, JMDBH, JMSG, JMFL, respectively). Additionally, correlations were calculated between juvenile height and mature volume (JHT-MVOL) and juvenile DBH and mature volume (JDBH-MVOL). Trait correlations were computed between all variables. Because the optimal rotation age for European black alder will depend on the management system used and the final product desired, juvenile-mature and trait correlation matrices were constructed for all available ages (i.e., age-age correlations). Correlations were computed between provenance means to indicate the reliability of provenance selection, and between all trees to indicate the reliability of mass selection.

RESULTS AND DISCUSSION

Age-age correlations based on provenance means generally were higher than those for single trees at rotations greater than 11 years. Single tree correlations were equal to or slightly higher than provenance correlations at younger ages (Tables 1.1a, b, c). Only slight differences existed between correlations for JMVOL (Table 1.1a) and JMDBH (Table 1.1c) for single trees or provenances. JMHT correlations (Table 1.1b) were slightly higher at younger selection ages, and slightly lower at older ages than JMDBH or JMVOL.

The JMHT correlations (Table 1.1b) were substantially lower than those reported for other species (Pinaceae-Lambeth 1980; red pine-Lester and Barr 1966; Scot's pine, Norway spruce-Nanson 1968; Scot's pine-Giertych 1974; southern pines-Wakeley 1971; slash pine-Squillace and Gansel 1974; slash pine-Allen 1977; ponderossa and western white pines-Steinhoff 1974; ponderossa pine-Namkoong and Conkle 1976; Douglas-fir-Namkoong et al. 1972; black walnut-Clausen 1982; black walnut-McKeand et al. 1979; black walnut-Kung 1975; hybrid poplar-Wilkinson 1974; cottonwood-Mohn and Randall 1971; aspen, poplar-Morhdiek 1979;). Using a cutoff point of r=0.7 to indicate a sufficiently strong correlation coefficient (r^2=.49 or approximately 50% of the variation is accounted for by the linear relationship between juvenile and mature performance (Steinhoff 1974)), early selection in European black alder should take place no sooner than one-half of the desired rotation age for height, DBH, or volume. These findings agree

Table 1.1. Age-age correlations for growth properties at 14 ages. Single tree correlations (N=42) are given above provenance correlations (N=14) for each selection age

Table 1.1a. Correlations for volume (JMVOL)

		ROTATION AGE												
		5	6	7	8	9	10	11	12	13	14	15	16	17
	4	.95	.90	.82	.74	.61	.53	.44	.33	.22	.15	.08	.04	.02
		.93	.83	.72	.62	.46	.37	.28	.19	.11	.06	.01	-.03	-.05
	5		.98	.93	.87	.75	.68	.59	.47	.35	.27	.20	.14	.11
S			.97	.91	.83	.69	.61	.52	.43	.35	.29	.24	.20	.17
E	6			.97	.92	.81	.74	.65	.53	.41	.32	.25	.20	.17
L				.96	.88	.76	.68	.60	.53	.44	.38	.33	.30	.28
E	7				.98	.90	.84	.76	.66	.54	.45	.38	.32	.29
C					.97	.90	.84	.78	.72	.64	.59	.54	.51	.48
T	8					.97	.93	.87	.78	.67	.59	.53	.47	.44
I						.97	.94	.90	.85	.79	.74	.70	.66	.64
O	9						.99	.95	.89	.81	.74	.69	.64	.60
N							.99	.97	.94	.89	.86	.83	.80	.78
	10							.99	.94	.88	.82	.77	.73	.70
A								.97	.99	.94	.91	.88	.86	.84
G	11								.98	.94	.90	.86	.83	.80
E									.99	.97	.95	.93	.91	.90
	12									.98	.96	.93	.91	.89
										.99	.98	.97	.95	.94
	13										.99	.98	.96	.95
											.99	.99	.98	.97
	14											.99	.99	.98
												.99	.99	.98
	15												.99	.99
													.99	.99
	16													.99
														.99

Table 1.1b. Correlations for height (JMHT)

		ROTATION AGE												
		5	6	7	8	9	10	11	12	13	14	15	16	17
	4	.85	.76	.74	.60	.44	.33	.26	.19	.19	.14	.05	.04	.02
		.89	.76	.66	.47	.26	.14	.06	-.02	-.07	-.07	-.13	-.15	-.16
	5		.92	.90	.79	.63	.55	.50	.42	.42	.36	.31	.28	.23
S			.94	.89	.73	.56	.47	.39	.32	.27	.26	.19	.16	.12
E	6			.94	.87	.74	.68	.61	.54	.53	.50	.45	.41	.36
L				.96	.86	.71	.67	.59	.53	.48	.49	.42	.39	.35
E	7				.92	.83	.78	.73	.64	.64	.59	.54	.50	.45
C					.92	.82	.79	.72	.65	.61	.60	.55	.51	.47
T	8					.93	.89	.85	.78	.76	.73	.68	.63	.57
I						.95	.91	.87	.79	.74	.75	.69	.65	.61
O	9						.96	.94	.88	.87	.84	.79	.74	.69
N							.97	.95	.89	.86	.85	.80	.75	.72
	10							.97	.92	.91	.89	.85	.80	.75
A								.99	.95	.93	.93	.90	.85	.81
G	11								.96	.95	.92	.89	.85	.79
E									.98	.96	.95	.93	.89	.86
	12									.99	.97	.95	.91	.86
										.99	.98	.96	.94	.91
	13										.98	.96	.93	.88
											.99	.98	.96	.93
	14											.98	.96	.93
												.99	.97	.95
	15												.99	.98
													.98	.96
	16													.99
														.99

Table 1.1c. Correlations for diameter at breast height (JMDBH)

		ROTATION AGE											
		5	6	7	8	9	10	11	12	13	14	15	16	17
	4	.92	.86	.80	.71	.52	.43	.36	.27	.18	.12	.06	.02	-.01
		.92	.87	.78	.65	.43	.32	.22	.15	.09	.02	-.01	-.05	-.08
	5		.98	.93	.85	.68	.59	.51	.42	.32	.23	.17	.12	.08
S			.98	.94	.83	.64	.54	.46	.41	.35	.29	.25	.21	.18
E	6			.96	.89	.73	.64	.56	.46	.36	.28	.21	.16	.13
L				.96	.86	.66	.58	.50	.44	.38	.32	.29	.24	.22
E	7				.97	.86	.79	.71	.61	.51	.42	.36	.31	.27
C					.96	.83	.77	.70	.65	.59	.53	.49	.45	.42
T	8					.95	.90	.84	.76	.67	.59	.54	.49	.45
I						.95	.91	.86	.82	.77	.71	.68	.64	.61
O	9						.99	.95	.90	.83	.77	.72	.68	.64
N							.99	.97	.94	.91	.87	.85	.81	.79
	10							.99	.95	.90	.85	.81	.77	.74
A								.99	.98	.95	.92	.91	.87	.85
G	11								.99	.95	.91	.88	.84	.82
E									.99	.98	.96	.94	.92	.90
	12									.99	.96	.94	.92	.89
										.99	.98	.97	.95	.93
	13										.99	.98	.96	.95
											.99	.99	.97	.96
	14											.99	.99	.98
												.99	.99	.98
	15												.99	.99
													.99	.99
	16													.99
														.99

with preliminary results reported for European black alder (Hall et al. 1983). But, in comparison, selection for height could take place as early as one-fifth the rotation age in the Pinaceae (Lambeth 1980) and one-third to one-half the rotation age in hybrid poplar (Wilkinson 1974) and cottonwood (Mohn and Randall 1971).

The low age-age correlations for growth characteristics could have been caused by several factors. First, the small variation in growth properties among trees yielded differences between provenances and trees that was relatively small, and this allowed significant changes in the rankings to occur throughout the 17-years of growth. Provenance tests usually contain widely diverse genotypes, and this normally can be expected to yield high age-age correlations because the trees segregate early and the rankings remain fairly constant (Steinhoff 1974; Giertych 1974). Second, provenances of European black alder have been shown to vary in rooting depth, width, and in root-to-shoot ratio (Schmidt-Vogt 1969). Trees that develop large, spreading root systems may lag behind in height and diameter growth initially. Then in later years, these trees may surpass the trees that had fast initial top growth, and consequently lower the age-age correlations. Finally, provenances that grow rapidly during their first years of growth have been noted for their rapid decline in later years (Funk 1979; Verweij 1977). This often has been attributed to the heavy flowering in these trees just prior to decline. This also could lead to changes in rankings, and ultimately, lower correlations.

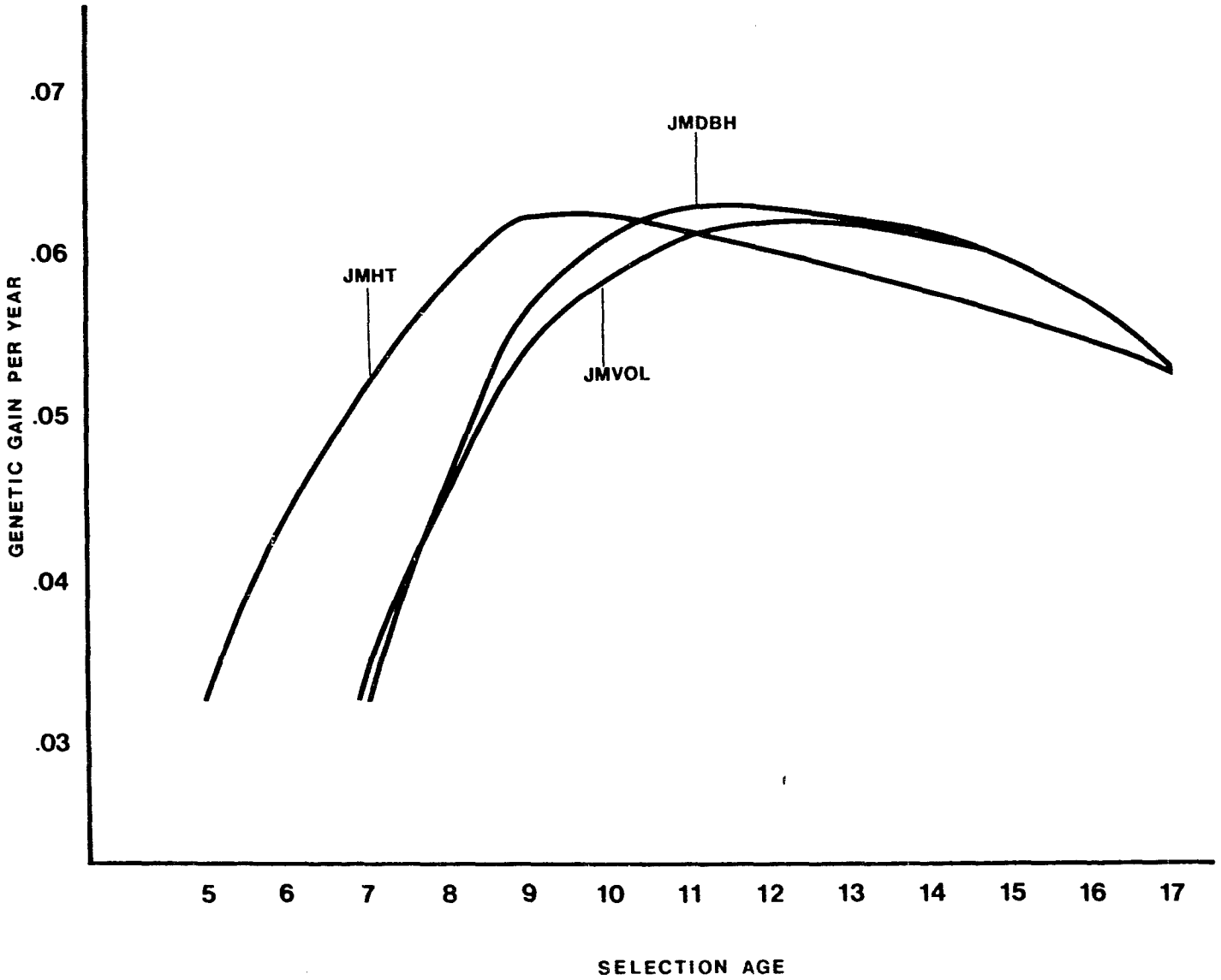
The selection age that optimizes genetic gain per year can be estimated using a technique developed by Squillace and Gansel (1974) and later discussed and employed by Lambeth (1980). The technique utilizes the relationship between genetic gain (G), age-age correlation ($r_{y,x}$), early selection age (T_y) and rotation age (T_x). T_y and T_x are the early selection age plus 2 years and the rotation age plus 2 years, respectively. The additional 2 years is the time period allotted for breeding, production, and establishment of seedlings. If G is the genetic gain realized by selection at the end of the rotation, then $Gr_{y,x}$ is the expected gain for selection at earlier ages. The genetic gain per year (G/year) at any early selection age based on a given rotation age is $G/year=Gr_{y,x}/T_y$. The efficiency of selection at a particular early selection age is $E=Gr_{y,x}T_x/T_y$. The efficiency values provide a means of comparing different early selection ages relative to a particular rotation age. No actual estimate of G is needed to compare the efficiency of selection at different ages because G is constant for a particular experiment.

For example, mass selection for height on a 17-year rotation gives G/year=1G/19=0.053G, but selection at age 10 gives G/year=0.75G/12=0.063G. The efficiency of selection at age 10 versus age 17 is therefore E=0.75G*19/12=1.19G. This indicates that selection at age 9 would yield 1.19 times more gain per year than selection at age 17.

Plotting gain per year by selection age reveals that the age for optimal mass selection occurs earlier for height than DBH or volume (Figure 1.1). However, the most important trait is volume which is difficult to measure directly. Height or DBH could be used to select for volume providing the correlations between the traits at the different ages are strong enough. Comparing the correlations between height and volume (JHT-MVOL) and DBH and volume (JDBH-MVOL) it can be seen that JDBH-MVOL has consistently higher correlations for a 17-year rotation than does JHT-MVOL (compare Tables 1.2a and 1.2b). The magnitude of this difference can be illustrated by comparing the plots of G/year (Figure 1.2). The optimal selection age using early height to predict volume occurs at a younger age than using DBH, but the gain per year using DBH is always greater. Therefore, early DBH is a better indicator of final volume because it yields greater gain per year. Although the optimal selection age using DBH to predict volume is at age 11, selections could be made as early as age 9 and still realize a better gain per year than if using height at age 9 or by waiting the entire rotation length to make selections

The preceding method assumes equal selection intensities at all ages. In reality, selection intensities could be significantly higher at earlier ages because the smaller trees allow increased planting densities and, therefore, more trees for selection (Falconer 1960; Nanson 1968; Lambeth 1980). In a theoretical evaluation of early selection in black walnut, Kung (1975) estimated that the most gain

Figure 1.1. Graph indicating maximum genetic gain per year using early selection for height (JMHT), DBH (JMDBH), and volume (JMVOL) on a 17-year rotation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GENETIC GAIN PER YEAR
JMDBH
JMHT
JMVOL
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SELECTION AGE

Table 1.2. Age-age correlations using early DBH and height to select for mature volume. Single tree (N=42) correlations are given above provenance correlations (N=14) for each selection age

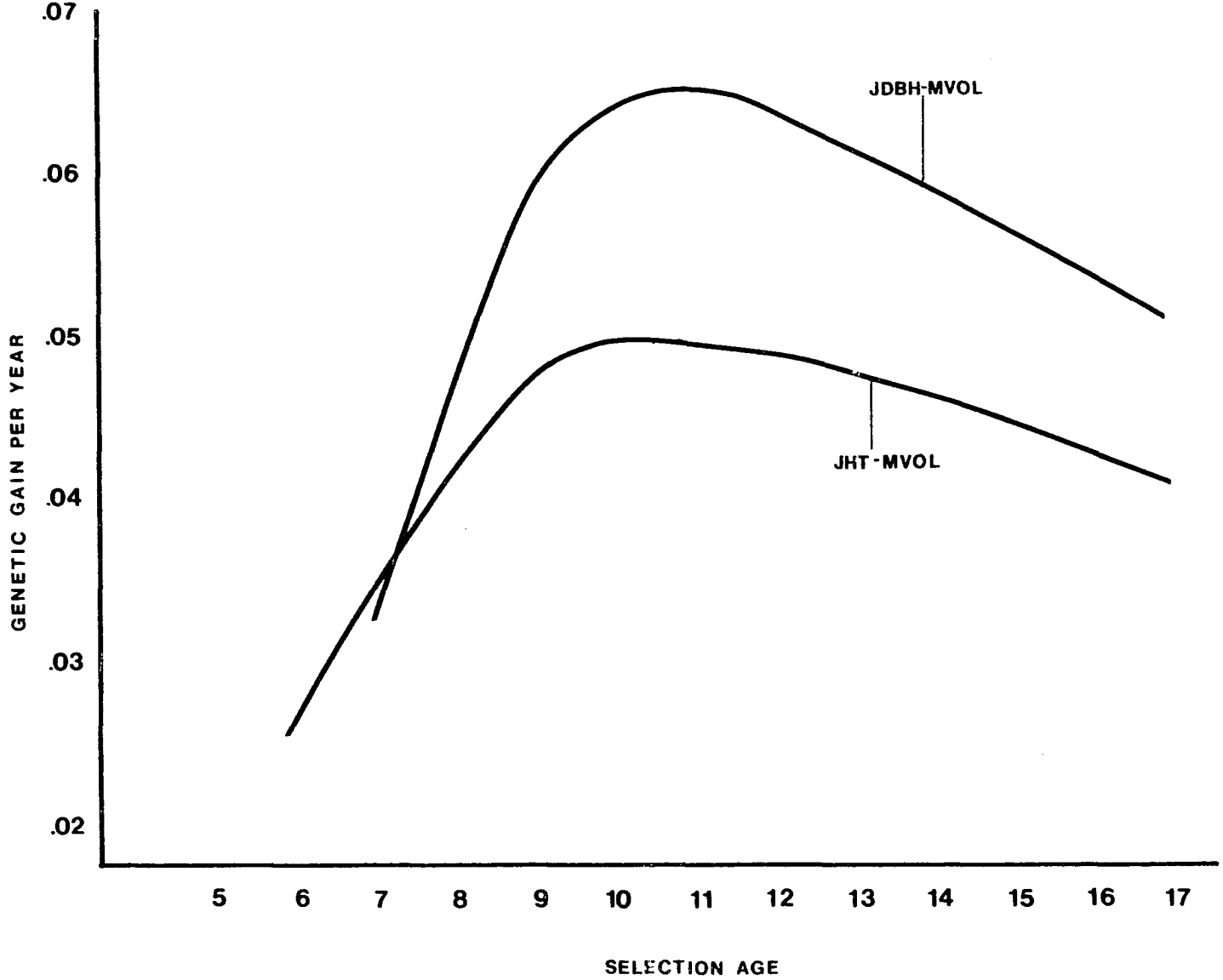
Table 1.2a. Correlations using DBH to select for volume (JDBH-MVOL)

	ROTATION AGE FOR VOLUME													
	4	5	6	7	8	9	10	11	12	13	14	15	16	17
4	.89	.86	.83	.78	.71	.59	.50	.42	.33	.23	.16	.10	.06	.04
	.90	.85	.78	.65	.54	.38	.28	.19	.11	.05	.00	-.05	-.08	-.09
5		.89	.90	.86	.81	.70	.62	.54	.44	.34	.26	.19	.14	.11
S		.87	.86	.78	.70	.57	.49	.41	.36	.30	.26	.22	.19	.17
E 6			.91	.88	.83	.74	.66	.58	.48	.38	.30	.24	.19	.16
L			.89	.82	.74	.61	.53	.46	.41	.35	.31	.27	.25	.24
E 7				.92	.91	.84	.78	.71	.62	.51	.43	.37	.32	.29
C				.91	.88	.79	.73	.67	.62	.57	.53	.49	.46	.45
E 8					.92	.90	.87	.81	.74	.66	.59	.53	.49	.46
T					.93	.90	.87	.82	.79	.75	.71	.68	.65	.64
I 9						.92	.92	.91	.87	.81	.76	.72	.68	.65
O						.95	.95	.93	.91	.89	.87	.85	.82	.81
N 10							.93	.94	.92	.88	.84	.80	.77	.74
							.96	.96	.95	.94	.92	.90	.88	.87
A 11								.94	.95	.93	.90	.88	.85	.83
G								.97	.98	.97	.96	.95	.93	.92
E 12									.95	.96	.94	.92	.91	.89
									.97	.98	.98	.97	.95	.95
F 13										.95	.95	.95	.94	.93
O										.97	.98	.97	.96	.96
R 14											.95	.95	.95	.94
											.97	.98	.97	.97
D 15												.95	.95	.95
B												.97	.97	.97
H 16													.95	.95
													.97	.98
17														.95
														.97

Table 1.2b. Correlations using height to select for volume (JHT-MVOL)

		ROTATION AGE FOR VOLUME												
		4	5	6	7	8	9	10	11	12	13	14	15	16	17
	4	.76	.74	.70	.64	.57	.45	.36	.28	.20	.12	.06	.02	-.02	-.04
		.72	.70	.65	.50	.35	.19	.09	-.01	-.04	-.09	-.13	-.17	-.20	-.21
S	5		.78	.79	.78	.73	.64	.56	.48	.40	.31	.25	.19	.14	.11
E			.78	.77	.71	.63	.51	.43	.36	.31	.27	.23	.19	.15	.13
L	6			.76	.75	.74	.67	.62	.55	.49	.41	.35	.29	.24	.20
E				.80	.79	.76	.68	.61	.54	.49	.44	.39	.35	.31	.29
C	7				.78	.80	.75	.71	.65	.58	.51	.45	.40	.34	.31
T					.80	.81	.76	.72	.66	.63	.60	.56	.53	.49	.47
I	8					.78	.78	.76	.72	.66	.60	.54	.49	.44	.41
O						.88	.85	.81	.76	.72	.67	.63	.59	.54	.52
N	9						.81	.81	.80	.76	.71	.66	.61	.56	.53
							.89	.89	.86	.83	.79	.76	.72	.68	.65
A	10							.84	.84	.81	.77	.73	.69	.64	.61
G								.91	.90	.88	.86	.83	.81	.77	.75
E	11								.83	.81	.76	.72	.69	.65	.62
									.92	.91	.89	.87	.85	.82	.80
F	12									.85	.82	.79	.76	.72	.70
O										.95	.94	.92	.90	.88	.87
R	13										.83	.81	.78	.75	.72
											.94	.93	.92	.90	.89
H	14											.79	.76	.74	.72
E												.89	.87	.86	.84
I	15												.77	.75	.74
G													.90	.89	.89
H	16													.76	.75
T														.90	.90
	17														.74
															.87

Figure 1.2. Graph indicating maximum genetic gain per year using early height or early DBH to select for volume on a 17-year rotation (JHT-MVOL, JDBH-MVOL respectively)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.06
.05
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.03
.02
GENETIC GAIN PER YEAR
JDBH-MVOL
JHT-MVOL
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9
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11
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SELECTION AGE

could be attained by selecting height at age 3 for volume at age 30. Age 3 proved better than other early selection ages because that particular combination of selection intensity and age-age correlation yielded the most gain.

Age-age correlations for wood properties were much higher than those for growth properties (Tables 1.3a and 1.3b). This is because, in most tree species, specific gravity and fiber length change predictably with age (Panshin and DeZeeuw 1980). In European black alder specifically, both of these characteristics increase with age (Robison 1984). The age-age correlations reflect this and indicate that selection for wood properties could take place much earlier than selection for growth properties. The plots of genetic gain per year reveal that for 17-year fiber length and specific gravity the optimal selection ages are 5- and 7-years, respectively (Figure 1.3).

The correlations between traits were variable depending on the traits compared and the ages at the time of comparison. The growth traits were all well-correlated with each other. At any given age, the correlations for DBH with volume were greater than for height with volume (compare Tables 1.2a and 1.2b). Correlations of height with DBH were lower still (Table 1.4). The correlations increased as the ratio of the selection age to rotation age decreased, and all were relatively high when the age ratio was 1.

The relationship between wood properties is more complex. The negative correlations between specific gravity and fiber length based on

Table 1.3. Age-age correlations for wood properties at 6 ages. Single tree correlations (N=39) are given above provenance correlations (N=13) for each selection age

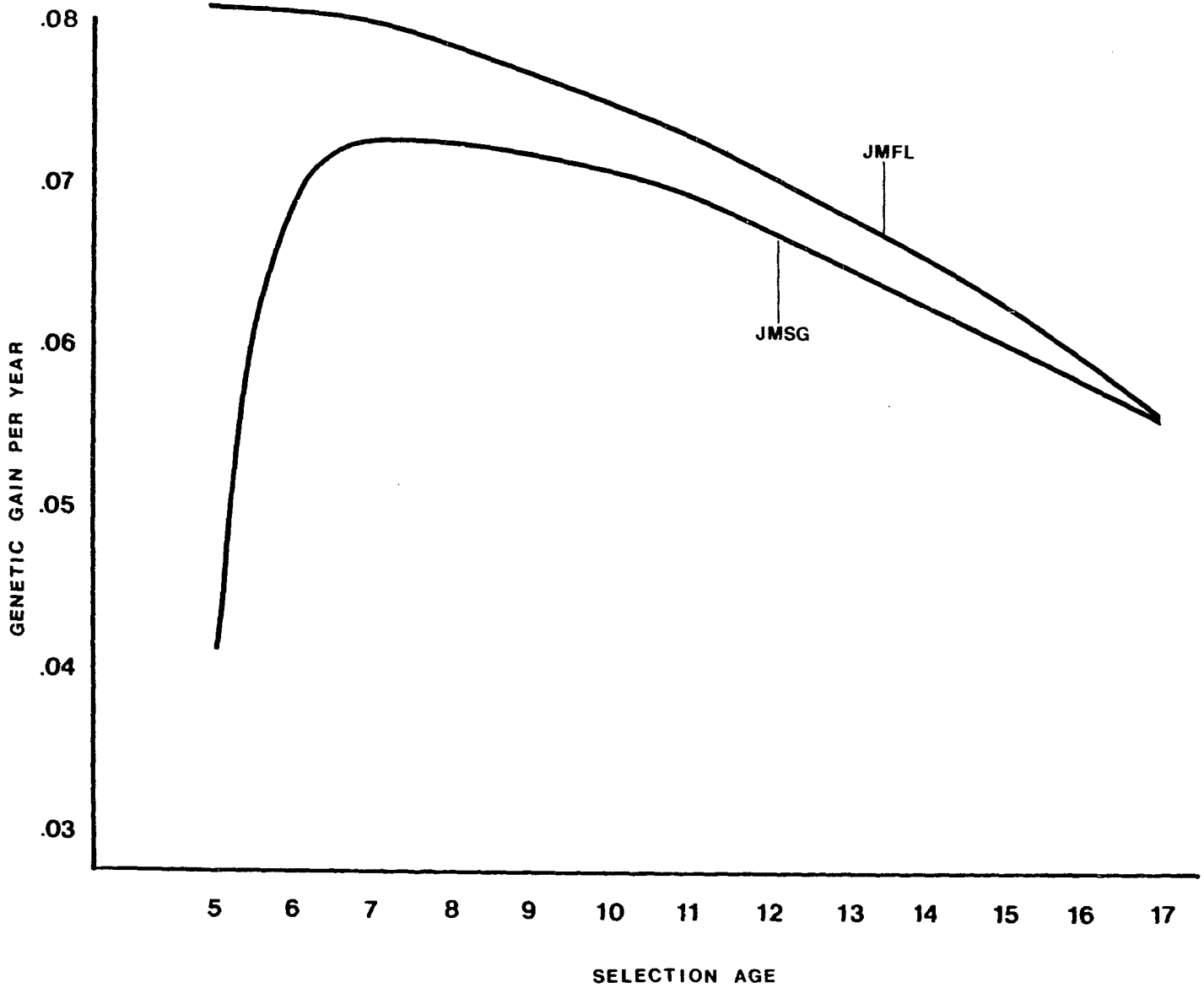
Table 1.3a. Age-age correlations for specific gravity

		ROTATION AGE				
		7	9	11	14	17
	5	.72	.57	.54	.41	.29
S		.71	.73	.79	.73	.51
E	7		.92	.86	.74	.65
L.			.94	.89	.83	.61
	9			.95	.88	.78
A				.93	.90	.74
G	11				.96	.87
E					.96	.81
	14					.95
						.91

Table 1.3b. Age-age correlations for fiber length

		ROTATION AGE				
		7	9	11	14	17
	5	.79	.71	.69	.61	.57
S		.75	.67	.63	.52	.49
E	7		.88	.85	.75	.71
L.			.89	.87	.74	.71
	9			.97	.90	.86
A				.98	.90	.87
G	11				.96	.93
E					.96	.94
	14					.98
						.99

Figure 1.3. Graph indicating maximum genetic gain per year using early selection for specifc gravity (JMSG) and fiber length (JMFL) on a 17-year rotation


.08
.07
.06
.05
.04
.03
GENETIC GAIN PER YEAR
JMFL
JMSG
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SELECTION AGE

Table 1.4. Correlations between height and DBH for 6 ages. Single tree correlations (N=42) are above provenance correlations (N=14) for each age

		HEIGHT					
		5	7	9	11	14	17
	5	.91	.84	.61	.47	.33	.21
		.93	.87	.56	.39	.27	.18
	7	.85	.86	.70	.63	.50	.39
D		.88	.91	.71	.61	.52	.43
B	9	.63	.77	.80	.80	.77	.67
H		.60	.85	.87	.90	.86	.81
	11	.47	.65	.77	.80	.83	.77
		.42	.74	.85	.92	.91	.87
	14	.23	.45	.62	.67	.77	.76
		.27	.60	.73	.84	.85	.85
	17	.08	.30	.47	.56	.70	.75
		.15	.49	.61	.76	.81	.85

provenance means indicate that provenance selection for either trait would deleteriously affect the other trait at most ages (Table 1.5). Correlations based on single trees indicate that mass selection for either trait would have a neutral or slightly positive effect on the other trait.

Provenance and single tree correlations between growth properties and specific gravity tend to be negative, and correlations between growth properties and fiber length tend to be positive especially at later ages (Table 1.6). However, most of these correlations are not significantly different from zero. This indicates that selection for growth properties should not adversely affect wood properties except at extremely early selection ages.

Table 1.5. Correlations between specific gravity and fiber length for 6 ages. Single tree correlatiions (N=39) are given above provenance correlations (N=13) for each age

		FIBER LENGTH					
		5	7	9	11	14	17
	5	.29	.17	.24	.25	.30	.28
S		-.28	-.38	-.15	-.15	.06	.06
P.	7	.07	.04	.08	.06	.05	.03
		-.61	-.61	-.58	-.55	-.39	-.36
G	9	.03	.04	.03	.02	.02	-.01
R		-.59	-.66	-.63	-.59	-.43	-.39
A	11	.05	.10	.15	.14	.16	.12
V		-.50	-.56	-.49	-.43	-.23	-.20
I	14	.00	.12	.18	.18	.22	.20
T		-.34	-.39	-.37	-.27	-.10	-.06
Y	17	-.01	.15	.23	.25	.29	.30
		-.23	-.17	-.16	-.05	.08	.14

Table 1.6. Correlations between growth and wood properties for 6 ages. Single tree correlations (N=39) are given above provenance correlations (N=13) for each age

		SPECIFIC GRAVITY						FIBER LENGTH					
		5	7	9	11	14	17	5	7	9	11	14	17
	5	.06	.11	.12	.06	.01	-.06	.26	.07	-.09	-.11	-.17	-.21
		-.46	-.31	-.16	-.26	-.29	-.33	.12	-.14	-.32	-.35	-.47	-.54
V	7	.08	.04	.02	.01	-.03	-.11	.30	.11	-.06	-.06	-.01	-.13
O		-.44	-.43	-.29	-.32	-.32	-.38	.27	-.05	-.18	-.18	-.28	-.34
L	9	.02	-.13	-.10	-.03	-.03	-.09	.35	.22	.10	.10	.08	.06
U		-.35	-.58	-.46	-.39	-.36	-.36	.51	.21	.19	.19	.13	.07
M	11	.00	-.20	-.14	-.03	.00	-.04	.30	.23	.17	.19	.21	.18
E		-.23	-.59	-.48	-.38	-.34	-.35	.54	.27	.32	.32	.30	.25
	14	.03	-.18	-.09	.06	.12	.10	.12	.14	.20	.24	.32	.31
		-.04	-.49	-.40	-.29	-.25	-.27	.47	.24	.38	.40	.43	.40
	17	.02	-.19	-.10	.04	.13	.14	.02	.07	.17	.24	.35	.35
		.01	-.43	-.36	-.23	-.19	-.18	.43	.23	.38	.42	.49	.48
	5	-.05	-.02	-.03	-.05	-.08	-.16	.23	.08	-.12	-.16	-.21	-.24
		-.43	-.24	-.24	-.36	-.37	-.38	.33	.02	-.18	-.23	-.33	-.39
H	7	.02	-.01	.01	.03	.03	-.05	.34	.17	.01	-.02	-.05	-.07
E		-.40	-.36	-.30	-.38	-.34	-.34	.52	.13	-.02	-.05	-.13	-.19
I	9	-.02	-.17	-.11	-.03	-.01	-.07	.41	.31	.19	.15	.12	.08
G		-.30	-.51	-.40	-.36	-.30	-.29	.65	.35	.25	.22	.12	.04
H	11	.02	-.20	-.16	-.04	.01	-.02	.37	.35	.28	.27	.26	.24
T		-.23	-.54	-.44	-.33	-.24	-.20	.69	.46	.44	.44	.38	.32
	14	.03	-.22	-.19	-.02	.05	.07	.33	.36	.37	.41	.46	.45
		-.21	-.56	-.50	-.32	-.24	-.15	.61	.50	.54	.57	.56	.51
	17	-.02	-.32	-.32	-.16	-.09	-.01	.16	.23	.26	.32	.40	.42
		-.27	-.57	-.54	-.36	-.28	-.12	.55	.49	.55	.58	.57	.56
	5	.12	.23	.23	.19	.13	.03	.28	.07	-.13	-.14	-.20	-.22
		-.32	-.03	.06	-.07	-.06	-.17	.04	-.27	-.51	-.48	-.52	-.54
	7	.11	.15	.15	.16	.12	.03	.30	.11	-.06	-.06	-.10	-.11
D		-.27	-.16	-.04	-.09	-.09	-.18	.16	-.21	-.35	-.30	-.31	-.35
B	9	-.06	-.19	-.15	-.07	-.06	-.10	.38	.23	.12	.13	.13	.12
H		-.32	-.50	-.42	-.37	-.32	-.30	.57	.21	.19	.20	.17	.12
	11	-.01	-.19	-.12	.00	.04	.00	.26	.20	.17	.21	.26	.24
		-.17	-.49	-.41	-.30	-.26	-.27	.51	.22	.30	.32	.33	.28
	14	.05	-.17	-.08	.06	.13	.11	.12	.12	.19	.25	.37	.36
		.01	-.39	-.33	-.21	-.17	-.20	.45	.18	.32	.35	.42	.40
	17	.03	-.18	-.11	.04	.13	.15	.01	.06	.16	.25	.39	.40
		.03	-.36	-.32	-.19	-.14	.13	.41	.20	.35	.41	.50	.50

LITERATURE CITED

Allen, P. J. 1978. Genotypic and phenotypic correlations of wood and tree characteristics. Pp. 184-196 in D. G. Nikles, J. Burles, and R. D. Barnes, eds. Proceedings of a joint workshop on Progress and Problems of Genetic Improvement of Tropical Forest Trees. Brisbane, Queensland, Australia, April 4-7, 1977. Dept. of Forestry, Commonwealth Forestry Inst., U. of Oxford, Great Britain.

Clausen, K. E. 1982. Age-age correlations in black walnut and white ash. Pp. 113-117 in B. A. Thielges, ed. Proceedings of the Seventh North American Forest Biology Workshop, "Physiology and Genetics of Intensive Culture", July 26-28, 1982. U. of Kentucky, Lexington, KY.

Falconer, D. S. 1960. Introduction to Quantitive Genetics. The Ronald Press Co., New York. 363pp.

Franklin, E. C. 1977. Juvenile-mature correlations. Pp. 205-212 in D. G. Nikles, J. Burley, and R. D. Barnes, eds. Proceedings of a joint workshop on Progress and Problems of Genetic Improvement of Tropical Forest Trees. Brisbane, Queensland, Australia, April 4-7, 1977. Dept. of Forestry, Commonwealth Forestry Inst., U. of Oxford, Great Britain.

Funk, D. T. 1973. Growth and development of alder plantings of Ohio strip-mine banks. Pp. 483-491 in R. J. Hutnick and G. Davis, ed. Ecology and Reclamation of Devastated Land. Vol. 1. Gordon and Breach, New York.

Funk, D. T. 1979. Alnus glutinosa provenance trials on Ohio strip mines: sixteen-year results. Pp. 28-32 in R. P. Guries, ed. Proceedings of the First North Central Tree Improvement Conference, Madison, WI, Aug. 21-23, 1979. U. of Wisconsin, Madison, WI.

Giertych, M. 1974. Inadequacy of early tests for growth characteristics as evidenced by a 59-year old experiment. Pp. 237-242 in Proceedings Joint IUFRO Meeting, Stockholm, 1974. Dept. of Forest Genetics, The Royal College of Forestry, Stockholm, Sweden.

Hall, R. B., G. A. Miller, T. L. Robison, and O. U. Onokpise. 1983. Developing Alnus for use in intensive culture. Pp. 35-45 in Intensive Plantation Culture:12 Years Research. U. S. D. A. Forest Service, North Central For. Exp. Stn., Gen. Tech. Rep. NC-91. North Central For. Exp. Stn., St. Paul, MN.

Kung, F. H. 1975. Development and use of juvenile-mature correlations in a black walnut tree improvement program. Pp. 243-249 in Proceedings of the 12th Southern Forest Tree Improvement Conference, June 12-13, 1973. Louisiana State University, Division of Continuing Education, Baton Rouge, LA.

Lambeth, C. C. 1980. Juvenile-mature correlations in Pinaceae and implications for early selection. Forest Sci. 26(4):571-580.

Lester, D. T. and G. R. Barr. 1966. Shoot elongation in provenance and progeny tests of red pine. Silvae Genetica 15(1):1-6.

McKeand, S., W. F. Beineke, and M. N. Todhunter. 1979. Selection age for black walnut progeny tests. Pp. 68-73 in R. P. Guries, ed. Proceedings of the First North Central Tree Improvement Conference, Madison, WI, August 21-23, 1979. U. of Wisconsin, Madison, WI.

Mohn, C. A. and W. K. Randall. 1971. Inheritance and correlation of growth characters in Populus deltoides. Silvae Genetica 20(5/6):182-184.

Mohrdiek, O. 1979. Juvenile-mature and trait correlations in some aspen and poplar trials. Silvae Genetica 28(2/3):107-111.

Namkoong, G. and M. T. Conkle. 1976. Time trends in genetic control of height growth in ponderosa pine. Forest Sci. 22(1):2-12.

Namkoong, G, R. A. Ursanis, and R. R. Silen. 1972. Age related variation in genetic control of height growth in Douglas-fir. Theor. Applied Gen. 42(4):151-159.

Nanson, A. 1968. Le valeur des tests precoces dans la selection des arbres forestiers en particulier au point de vue de la croissance. Disser. Doct. Gembloux Sta. Rech. Eaux et For., Groenendall-Hoeillart, H. S. No. 38. 242pp.

Nanson, A. 1970. Juvenile and correlated trait selection and its effect on selection programs. Pp. 17-26 in Papers presented at the second meeting of the working group on quantitative genetics, Section 22, IUFRO, Raleigh, NC, August 18-19, 1969. Southern Forest Exp. Stn., New Orleans, LA.

Panshin, A. J. and C. DeZeeuw. 1980. Textbook of Wood Technology. Fourth Edition. McGraw-Hill Book Company. New York.

Rehfeldt, G. E. 1983. Genetic variability within Douglas-fir populations: implications for tree improvement. Silvae Genetica 32(1/2):9-14.

Robison, T. L. 1984. Age-age correlations, trait correlations, and wood property variation for an Alnus glutinosa (L.) Gaertn. provenance study. Ph. D. Dissertation. Iowa State University, Ames, Iowa. 81pp.

Robison, T. L. and R. B. Hall. 1981. Approaches to European alder improvement. Pp. 65-77 in R. P. Guries, ed. Proceedings of the Second North Central Tree Improvement Conference, Lincoln, NE.

Schmidt-Vogt, H. 1969. Growth and root development in Alnus glutinosa of different provenances. Pp. 725-731 in Proc. Second World Consultation on Forest Tree Breeding. Washington, D. C. FO-FTB:69-6/12.

Squillace, A. E. and C. R. Gansel. 1974. Juvenile-mature correlations in slash pine. Forest Sci. 20(3):225-229.

Steinhoff, R. J. 1974. Juvenile-mature correlatins in ponderosa and western white pines. Pp. 243-250 in Proceedings Joint IUFRO Meeting, Stockholm, 1974. Dept. of Forest Genetics, The Royal College of Forestry, Stockholm, Sweden.

Verweij, A. A. 1977. [Research on provenances and progenies of alder (Alnus glutinosa, Alnus incana, and Alnus cordata)]. Rijksinstituut voor onderzoek in de bosen landschapsboow "De Dorschkamp," Wageningen. Uitvoerig verslag. 15(1):1-23. (Dutch with English summary and captions).

Wakeley, P. C. 1971. Relation of thirtieth-year to earlier dimensions of Southern pines. Forest Sci. 17(2):200-209.

Wilkinson, R. C. 1974. Realized and estimated efficiency of early selection in hybrid poplar clonal tests. Pp. 26-32 in P. W. Garrett, ed. Proceedings of the 21st Northeastern Forest Tree Improvement Conference. Fredericton, New Brunswick. August 27-30, 1973.

SECTION II. SPECIFIC GRAVITY AND FIBER LENGTH VARIATION IN AN ALNUS GLUTINOSA (L.) GAERTN. PROVENANCE STUDY

INTRODUCTION

European black alder (Alnus glutinosa (L.) Gaertn.) has the potential to be utilized for lumber, composites, pulp, or biomass for energy. To identify sources of this species with desirable characteristics for these uses, information on the variation in wood quality characteristics is needed. Two important characteristics are specific gravity and fiber length.

Specific gravity is the best overall indicator of wood quality because it is directly related to solid wood strength, compressibility of composite furnish, pulp yields, and fuel value. Fiber length is used as an indicator of strength properties of paper.

Previous studies state that average stem specific gravity in European black alder ranges from 0.43 (Vurdu and Bensend 1979) to 0.49 (Morin 1974) in older trees, or from 0.30 to 0.40 in two-year-old material (Kellison and White 1979; Geyer 1981). Average fiber length has been reported at 0.89 mm (Bruun and Sluungaard 1957) or varying from 0.89 mm to 0.80 mm from bottom to top of stems (Vurdu and Bensend 1979) in older trees, respectively. The range in the two-year-old trees was from 0.95 mm to 1.33 mm. However, these studies were based on small sample sizes of unknown or very limited genetic background.

The purpose of this study was to clarify and add to the data base available on specific gravity and fiber length for European black alder. Variation in these traits within and among trees and provenances and also over time are discussed. Additionally, a small study was done to

determine if breast height samples can be used to estimate whole-tree properties as an indication of whether increment core samples would have predictive value.

MATERIALS AND METHODS

Thirty-nine trees from a provenance test located on a coal spoil in Ohio were analyzed in this study (Funk 1973; 1979). These trees represented 13 of the original 15 provenances in Funk's study (Table 2.1). The provenance test was arranged in a randomized complete block design with 3 replications. One tree was harvested from each provenance in each block.

Data obtained from a stem analysis study on these trees (Robison 1984) provided information allowing 5 disks, 2 cm thick to be removed at variable heights along each stem. The 5 disks in each tree contained 14, 12, 10, 8, and 6 annual rings respectively. Four wedges were cut from each disk avoiding branch traces when possible. Two were used for specific gravity determinations and 2 for fiber length measurements. Each wedge was subdivided into growth segments along rings corresponding to ages 5, 7, 9, 11, 14, and 17 years (Figure 2.1). Each growth segment was labeled using a coordinate system developed by Balodis (1966). This sampling procedure was used so that comparisons between trees were based on wood of similar physiological age (Richardson 1961). The variability of wood within a tree is caused by physiological gradients originating in the crown and proceeding down the stem (Larson 1969). Statistical sampling, therefore, should take into consideration these biological variation patterns (Richardson 1961; Larson 1969). Because of the relationship between the growing tips that regulate cell formation and a particular position in a tree, it was assumed that disks with the same

Table 2.1. Provenance locations and their latitude of origin. (Adapted from Funk (1973))

No.	Location	Latitude (N)
18	Ysenburger Hedges, Germany	50°09'
24	Danndorf, Germany	52°31'
28	Dietz, Germany	50°23'
43	Havno Lounkiaer, Denmark	56°43'
44	Spreewald, Germany	52°00'
45	Sulzschneid, Germany	47°43'
46	Graasten, Germany	54°55'
48	Danndorf, Germany	52°31'
49	Wasserburg, Germany	48°03'
53	Antwerp, Belgium (plantation)	51°13'
54	Uetze, Germany	52°28'
56	Diessen, Germany	47°57'
58	Kaufbeuren, Germany	47°52'

ring numbers in each tree were more likely to be formed at similar physiological stages than disks removed at fixed intervals along the stems.

The maximum moisture content method was used to determine specific gravity (Smith 1954). However, instead of using a vacuum, samples were boiled to speed water saturation. The specific gravity was determined by the formula:

$G_f=1/(((M_m-M_o)/M_o+(1/G_{so}))$ where

G_f=specific gravity based on green volume

M_m=weight of saturated wood sample

M_o=weight of oven-dried wood sample

G_{so}=average density of wood substance=1.53.

Samples for fiber length measurements were macerated in a 1:1 solution of glacial acetic acid and 30% hydrogen peroxide for 24 hours at 60° C then rinsed 3 times in distilled water. For each sample, a drop of macerated tissue was placed on a microscope slide, stained with Safrinin, and covered. The slide then was placed in a slide holder fitted into a Carousel projector and projected onto a flat screen. Fifteen whole fibers per sample were measured to the nearest 1 mm at 90x magnification.

Fiber length ring segment samples were weighted by the areas each ring segment represented in the disk from which they were removed, and

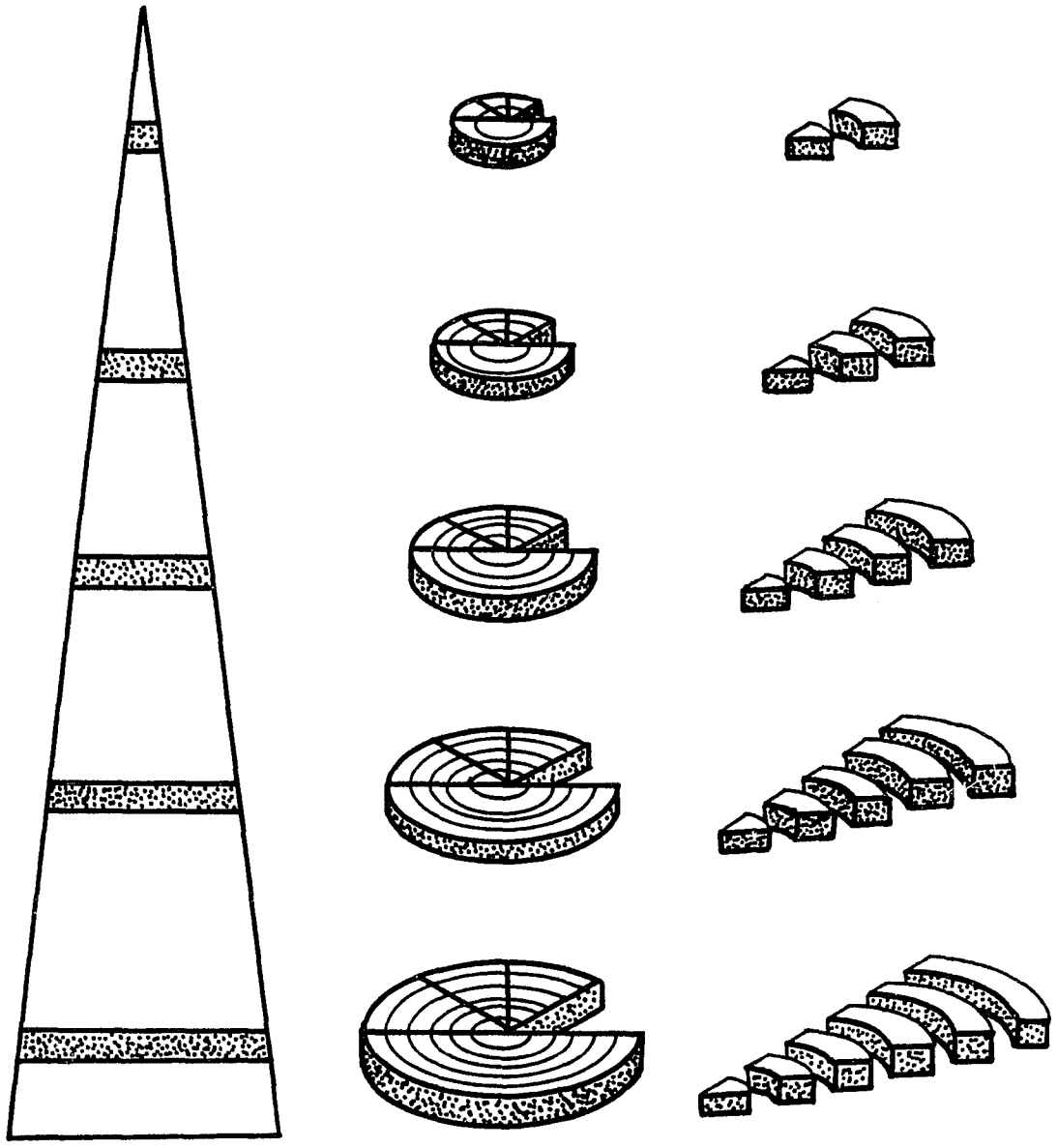

Figure 2.1. Sampling scheme for specific gravity and fiber length determinations. Five disks were removed from each stem (left), four wedges cut from each disk (center), and divided along growth rings representing years 5, 7, 9, 11, 14, and 17 (right)

the height that the disk represented in the tree, which is the distance half-way above and below the disk to the next respective disks. For specific gravity, weights of successive ring segments in a disk were summed to give saturated and dry weight values for the combined ring segments. For example, for year 9 on the lower disk, saturated weights and then dry weights were summed for the inner 3 ring segments to obtain saturated and dry weight values to calculate specific gravity for year 9. This value then was weighted by the height the lower disk represented in the tree. This value then was combined with similarly obtained values from the next 2 higher disks to obtain a whole tree specific gravity estimate for age 9. This weighting scheme was used to provide specific gravity and fiber length estimates of whole tree values for ages 5, 7, 9, 11, 14, and 17. These values for whole-tree specific gravity and fiber length were used in analysis of variance to determine if significant differences existed among provenances for these traits, and to calculate correlations with latitude to determine if these traits varied predictably with geographic origin.

Because disks were sampled at variable heights along each stem, not all trees had disks sampled from breast height. However, specific gravity and fiber length data at breast height were collected from 10 trees. The breast height data were used to compare with whole tree values to give an indication of the merit of using breast height increment core samples to estimate whole tree values.

RESULTS AND DISCUSSION

Specific gravity based on provenance means ranged from 0.37 to 0.42 depending on the age and origin of the material (Table 2.2). Individual tree values had a wider range as expected, and varied from 0.33 to 0.50. There were no significant differences among provenances at any age (Table 2.3).

Averaged over all trees specific gravity generally increased across disks from the pith outwards except in the lower 2 disks where there was an initial decrease followed by an increase in specific gravity. Specific gravity increased with height in the outermost ring segment (youngest wood), initially increased then decreased in the middle 3 ring segments, and decreased slightly in the innermost ring segment (oldest wood) (Figure 2.2).

Mean provenance fiber length ranged from 0.68 mm to 1.01 mm with individual tree values ranging form 0.58 mm to 1.09 mm (Table 2.4). The differences also were related to the age of the wood. As was found for specific gravity, whole tree fiber length did not vary significantly among provenances at any age (Table 2.5).

Fiber length variation across disks and within ring segments followed a more predictable pattern than did specific gravity. Fiber length averaged over all trees increased from pith to bark in all disks, and decreased from the base of the tree upwards in all ring segments (Figure 2.3).

Table 2.2. Mean provenance specific gravity and minimum and maximum individual tree specific gravity for 6 ages of Alnus glutinosa

PROVENANCE	AGE 5	7	9	11	14	17
46	.42(.009)[a]	.42(.006)	.42(.012)	.41(.005)	.41(.005)	.42(.002)
28	.39(.010)	.39(.007)	.40(.003)	.40(.003)	.40(.008)	.41(.011)
48	.38(.016)	.40(.003)	.40(.006)	.39(.008)	.40(.011)	.40(.011)
58	.41(.018)	.41(.018)	.40(.019)	.40(.018)	.40(.020)	.41(.017)
18	.42(.036)	.40(.020)	.39(.016)	.40(.014)	.40(.011)	.41(.010)
49	.38(.024)	.40(.013)	.39(.012)	.39(.011)	.39(.009)	.40(.007)
56	.38(.010)	.37(.010)	.37(.009)	.38(.009)	.39(.005)	.40(.005)
44	.38(.018)	.38(.012)	.38(.012)	.39(.014)	.39(.016)	.39(.018)
24	.39(.005)	.40(.008)	.39(.004)	.39(.002)	.39(.002)	.39(.005)
43	.41(.045)	.39(.011)	.39(.002)	.39(.004)	.39(.005)	.39(.001)
53	.40(.014)	.40(.017)	.40(.017)	.39(.017)	.39(.017)	.39(.018)
45	.39(.015)	.39(.010)	.39(.011)	.38(.008)	.39(.003)	.39(.007)
54	.37(.009)	.38(.016)	.37(.017)	.37(.018)	.38(.022)	.39(.023)
Overall mean	.39	.40	.39	.39	.39	.40
Individual tree:						
Minimum	.33	.34	.34	.34	.33	.34
Maximum	.50	.44	.45	.44	.44	.44

[a]Specific gravity (standard error of the mean).

Table 2.3. Analysis of variance for whole-tree fiber length at 6 ages. No F values were significant at the .01 level

		AGE											
		5		7		9		11		14		17	
Source	df	SS	F	SS	F	SS	F	SS	F	SS	F	SS	F
Replication	2	.0009	.33	.0002	.02	.0006	.65	.0007	.81	.0011	1.25	.0016	1.84
Provenance	12	.0106	.65	.0064	1.05	.0054	.99	.0033	.68	.0027	.59	.0035	.68
Error	24	.0328		.0122		.0108		.0097		.0101		.0104	

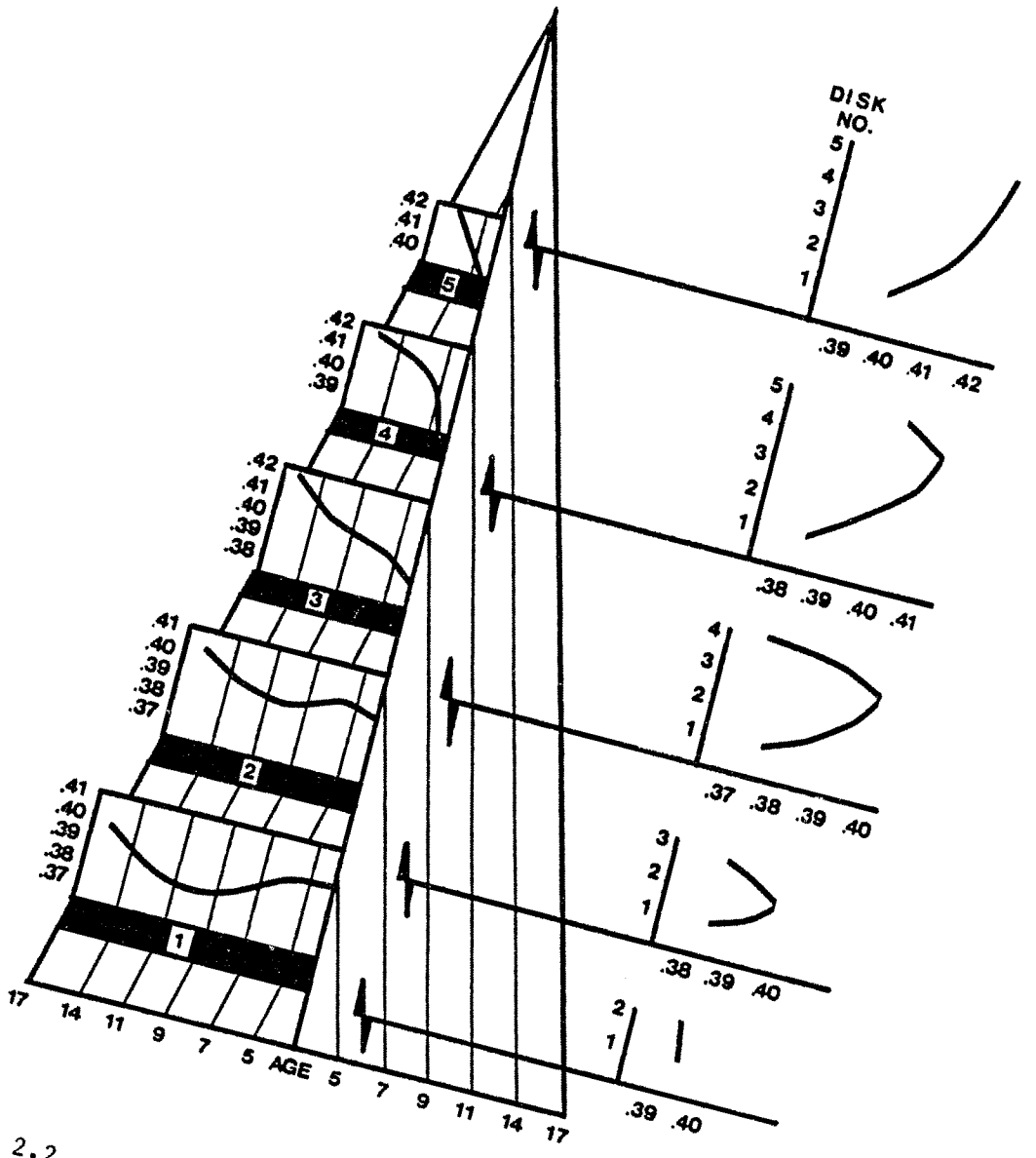

Figure 2.2. Radial variation in average specific gravity at five heights (left), and axial variation in five growth segments (right) for Alnus glutinosa

Table 2.4. Mean provenance fiber length and maximum and minimum individual tree fiber length for 6 ages of Alnus glutinosa

PROVENANCE	AGE 5	7	9	11	14	17
56	.74(.063)[a]	.88(.055)	.92(.042)	.95(.034)	.98(.028)	1.01(.024)
18	.73(.032)	.82(.012)	.90(.036)	.92(.038)	.97(.042)	1.00(.040)
28	.71(.026)	.79(.007)	.85(.010)	.89(.008)	.93(.012)	.96(.012)
58	.72(.035)	.80(.012)	.84(.010)	.87(.000)	.92(.005)	.95(.005)
49	.70(.060)	.79(.064)	.85(.070)	.87(.071)	.90(.077)	.93(.082)
45	.70(.039)	.78(.033)	.83(.019)	.86(.017)	.91(.024)	.93(.025)
43	.68(.054)	.78(.032)	.85(.031)	.86(.034)	.90(.036)	.93(.040)
54	.75(.035)	.83(.018)	.87(.014)	.88(.016)	.90(.017)	.92(.019)
48	.68(.037)	.79(.035)	.83(.042)	.85(.041)	.88(.036)	.91(.038)
24	.67(.039)	.78(.012)	.84(.012)	.86(.023)	.90(.038)	.91(.041)
44	.72(.039)	.79(.018)	.85(.017)	.87(.014)	.89(.019)	.91(.017)
46	.69(.010)	.77(.008)	.82(.015)	.84(.012)	.87(.019)	.89(.028)
53	.71(.010)	.78(.030)	.83(.014)	.84(.010)	.86(.016)	.88(.018)
Overall mean	.71	.80	.85	.87	.91	.93
Individual tree:						
Minimum	.58	.71	.75	.79	.79	.81
Maximum	.86	.99	1.00	1.02	1.05	1.09

[a]Fiber length in millimeters (standard error of the mean).

[b]Standard error of the mean is less than .0005.

Table 2.5. Analysis of variance for whole-tree fiber length at 6 ages. No F values were significant at the .01 level

		AGE											
		5		7		9		11		14		17	
SOURCE	df	SS	F	SS	F	SS	F	SS	F	SS	F	SS	F
Replication	2	.0162	1.81	.0066	1.17	.0057	1.00	.0042	.74	.0062	.92	.0081	1.09
Provenance	12	.0207	.38	.0320	.94	.0323	.95	.0348	1.03	.0450	1.12	.0546	1.23
Error	24	.1078		.0679		.0684		.0678		.0804		.0891	

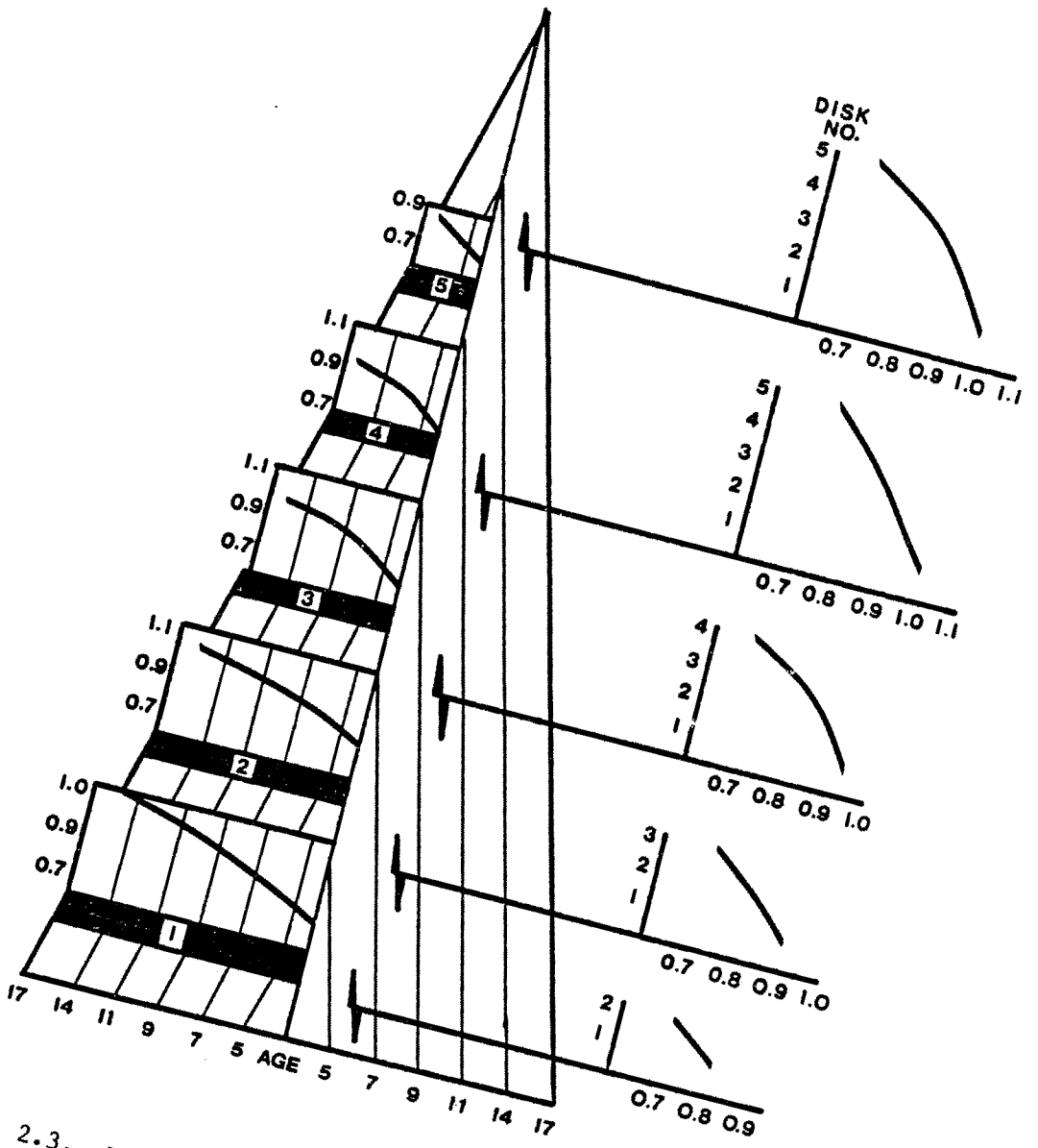

Figure 2.3. Radial variation in average fiber length at five heights (left), and axial variation in five growth segments (right) for Alnus glutinosa

The increase in average fiber length across disks is common to most tree species. This probably is related to the negative correlation between the rate of anticlinal divisions and fusiform initial length (Philipson and Butterfield 1967). When a decrease in cell division rate occurs, the fusiform initials remain in the elongation period longer. The longer initials subsequently produce longer fibers. The decrease in fiber length from the base of the tree upwards probably is related to this phenomenon, also. The width of a particular ring in a tree widens from the base to the top. This widening is indicative of faster growth, more anticlinal divisions, and in turn shorter fibers.

Correlations between specific gravity and latitude of provenance origin were consistently positive, and those between fiber length and latitude were consistently negative (Table 2.6). This suggests that northern sources produce denser wood and southern sources produce longer fibers. However, none of these correlations were significant, and no significant differences among provenances in either trait were found. Based on these results, improvement in these traits could not be accomplished by selection based on geographic origin. However, it must be stressed that the provenances used in this study represent a limited part of European black alder's natural range. A more thorough sampling may indeed uncover significant variation related to seed origin.

The overall mean values for fiber length and specific gravity in this study are somewhat lower than those reported previously by Morin (1974) and Vurdu and Bensend (1979) although single tree values were, in

Table 2.6. Correlations of specific gravity (SG) and fiber length (FL) with latitude of provenance origin for 6 ages. Single tree correlations (N=39) are given above provenance correlations (N=13) for each age

		SG	FL
	5	.10	-.17
A		.22	-.44
	7	.14	-.24
G		.24	-.44
	9	.20	-.20
E		.33	-.36
	11	.11	-.27
		.21	-.46
	14	.05	-.30
		.09	-.50
	17	.02	-.31
		.04	-.51

some instances, greater. The differences probably resulted from random sampling variation because of the small sample sizes used in the previous studies. The trees used in the present study were grown on a coal spoil, and the resulting site factors and poor growth may have resulted in lower values, although from the previous discussion on cell division rate it would seem likely that the fibers would be longer because of the slow growth. Decreases in specific gravity and fiber length with slow growth have been noted in Populus and Eucalyptus, and it is generally accepted that diffuse-porous hardwoods do not behave in the same manner as the conifers and ring-porous hardwoods on which most of the developmental studies have been done (Panshin and DeZeeuw 1980). It is difficult to predict the effect a coal spoil environment would have on the quality of wood produced from the trees grown there because no studies have been done on this matter. Fusiform initial abortion could be high because of severe water stress and aluminum toxicity. Cell elongation and cell wall formation also could be restricted for the same reasons. These factors could contribute to reduced specific gravity and fiber length.

Increment cores taken at breast height potentially can be used to estimate whole tree specific gravity and fiber length based on the correlations between breast height data and whole tree estimates (Tables 2.7a, b). The correlation between increment core and whole-tree values also has been found significant for many other species (Mitchell 1958; Wahlgren and Fassnacht 1959; Zobel et al. 1960; Boyce and Kaeiser 1960;

Table 2.7. Correlations of specific gravity and fiber length estimates at breast height with whole-tree estimates at 6 ages (N=10)

Table 2.7a. Correlations for specific gravity

		WHOLE TREE AGE					
		5	7	9	11	14	17
B	5	.99	.61	.56	.66	.47	.18
H	7		.95	.96	.93	.84	.71
	9			.95	.78	.75	.65
A	11				.82	.85	.75
G	14					.85	.75
E	17						.77

Table 2.7b. Correlations for fiber length

		WHOLE TREE AGE					
		5	7	9	11	14	17
B	5	1.00	.79	.76	.82	.89	.86
H	7		.99	.94	.93	.89	.85
	9			.98	.96	.87	.83
A	11				.99	.93	.90
G	14					.96	.95
E	17						.98

Einspahr et al. 1962; Core et al. 1978; Brazier and Howell 1979).

Heritabilities generally have been on the order of 0.40 or more for both specific gravity and fiber length for other species studied (Wilcox 1977; Namkoong et al. 1969; Smith 1967), therefore genetic improvement for these traits seems feasible. Because there was no significant variation among the provenances sampled in this study, it is recommended that mass selection be used initially to improve these traits. Sampling more seed sources from throughout the native range of European black alder may reveal significant variation among provenances, but results from most studies agree that large tree-to-tree variation in wood properties overshadows provenance variation (Einspahr et al. 1962). Provenances could first be identified with superior growth properties and adaptability, then mass selection for specific gravity and fiber length could be used to select superior trees from within this group.

LITERATURE CITED

Balodis, V. 1966. Co-ordinate systems based on the age of growth rings and internodes in trees. J. Inst. Wood Sci. 16:35-42.

Boyce, S. G. and M. Kaeiser. 1960. Small increment cores can be use for sampling cottonwood fibers. J. For. 58(6):484-485.

Brazier, J. D. and R. S. Howell. 1979. The use of breast-height core for estimating selected whole tree properties of sitka spruce. Forestry 52(2):177-185.

Bruun, H. H. and S. Sluungaard. 1957. Investigations of porous wood as pulp raw material. 1. Fiber lengths of the species Alnus glutinosa (L.) Gaertn., Alnus incana (L.) Moench, Betula verrucosa Ehrn., and Populus tremula (L.). Papper och Tra 39(11):521-525.

Core, H. A., W. W. Moschler, and C. Chang. 1978. A note on prediction of wood properties in yellow-poplar. Wood and Fiber 9(4):258-261.

Einspahr, D. W., J. P. van Buijtenen, and E. F. Thor. 1962. Wood and pulp properties determined from slash pine increment core and whole tree measurments. Silvae Genetica 11(3):68-77.

Funk, D. T. 1973. Growth and development of alder plantings of Ohio strip-mine banks. Pp. 483-491 in R. J. Hutnick and G. Davis, ed. Ecology and Reclamation of Devastated Land. Vol. 1. Gordon and Breach, New York.

Funk, D. T. 1979. Alnus glutinosa provenance trials on Ohio strip mines: sixteen-year results. Pp. 28-32 in R. P. Guries, ed. Proceedings of the First North Central Tree Improvement Conference, Madison, WI, Aug. 21-23, 1979. U. of Wisconsin, Madison, WI.

Geyer, W. A. 1981. Growth, yield and woody biomass characteristics of seven short-rotation hardwoods. Wood Sci. 13(4):209-215.

Kellison, R. C. and G. White. 1979. Black alder performance in the Southeast. Pp. 345-355 in J. C. Gordon, C. T. Wheeler, and D. A. Perry, eds. Proceedings of a Workshop, "Symbiotic Nitrogen Fixation in the Management of Temperate Forests," April 2-5, 1979. Oregon State University, Corvallis, Oregon.

Larson, P. R. 1969. Wood formation and the concept of wood quality. Yale Univ. School of Forestry Bulletin No. 74. Yale Univ., New Haven, CN. 54pp.

Mitchell, H. L. 1958. Wood quality evaluation from increment cores. TAPPI 41(4):150-156.

Morin, M. J. 1974. NSSC pulping of young European black alder (Alnus glutinosa L. Gaertn.) TAPPI 57(6):133-135.

Namkoong, G., A. C. Barefoot, and R. G. Hitchings. 1969. Evaluating control of wood quality through breeding. TAPPI 52(10):1935-1938.

Panshin, A. J. and C. DeZeeuw. 1980. Textbook of Wood Technology. Fourth Edition. McGraw-Hill Book Company. New York.

Philipson, W. R. and B. G. Butterfield. 1967. A theory on the causes of size variation in wood elements. Phytomorphology 17(1/4):155-159.

Richardson, S. D. 1961. A biological basis for sampling in studies of wood properties. TAPPI 44(3):170-173.

Robison, T. L. 1984. Age-age correlations, trait correlations, and wood property variation for an Alnus glutinosa (L.) Gaertn. provenance study. Ph. D. Dissertation. Iowa State University, Ames, Iowa. 81pp.

Smith, D. M. 1954. Maximum moisture content method for determining specific gravity of small wood samples. U. S. D. A. Forest Service FPL Report No. 2014. Forest Products Lab., Madison, WI. 3pp.

Smith, W. J. 1967. The heritability of fiber characteristics and its application to wood quality improvement in forest trees. Silvae Genetica 16(2):41-51.

Vurdu, H. and D. W. Bensend. 1979. Specific gravity and fiber length in European black alder roots, branches, and stems. Wood Sci. 12(2):103-105.

Wahlgren, H. E. and D. L. Fassnacht. 1959. Estimating tree sppecific gravity from a sinngle increment core. U. S. D. A. Forest Products Lab. Rep., Tech. Publ. No. 2146. Forest Products Lab., Madison, WI. 9pp.

Wilcox, M. D. 1977. Some problems in selection to improve wood properties. Pp. 213-225 in D. G. Nikles, J. Burley, and R. D. Barnes, eds. Proceedings of a joint workshop on Progress and Problems of Genetic Improvement of Tropical Forest Trees. Brisbane, Queensland, Australia, April 4-7, 1977. Dept. of Forestry, Commonwealth Forestry Inst., U. of Oxford, Great Britain.

Zobel, B., F. Henson, and C. Webb. 1960. Estimation of certain wood properties of loblolly and slash pine trees from breast-height sampling. Forest Sci. 6(2):155-162.

OVERALL SUMMARY AND DISCUSSION

General

This dissertation reports findings on age-age correlations, trait correlations, and wood property variation for European black alder. The age-age correlations for height, diameter, and volume revealed that selection at one-half the rotation length yielded the greatest genetic gain per year for a 17-year rotation. For specific gravity and fiber length, the greatest gain would occur from selection at one-third the rotation age.

The wide variability in the wood quality traits suggested that genetic improvement was indeed possible based on published reports for heritabilities in other species and using mass selection. Provenance selection did not look promising because of nonsignificant variation among provenances for these traits. However, because the provenances in this study represented a limited geographic range, it is suggested that a wider selection of provenances be sampled to conclusively determine whether or not significant provenance variation exists for these traits in this species.

Correlations between all traits showed that only in the case of provenance selection for specific gravity and fiber length did significant negative correlations exist. Nonsignificant, but fairly consistent negative correlations were obtained between growth properties and specific gravity. It is likely that specific gravity will be included in improvement programs for European black alder. By regularly

screening individuals for specific gravity, trees selected for good growth properties but having low specific gravity can be rogued. Additionally, periodic screenings for fiber length should reveal provenances that are desirable for both specific gravity and fiber length.

Further Comments on Early Selection

This study utilized phenotypic correlations to estimate the relationship of a trait at early and later ages. There is no doubt that estimates of genetic correlations and juvenile and mature heritabilities would give more reliable prediction of genetic gain. But even if these genetic parameters are available, they still must be of sufficient magnitude to permit sufficient gain using early selection.

Some traits have higher age-age corelations and heritabilities than others, and these lend themselves well to early selection based on these correlations. Specific gravity and fiber length are two such traits. Additionally, these two characteristics increase with age. Since higher specific gravity and longer fibers are usually desirable, selection could begin at a very early age to improve these traits.

The method of using age-age correlations requires measurement of a trait throughout the rotation, or at least a significant part of it. This requires a large investment in time. It has been suggested that age-age correlations are predictable (Lambeth 1980). Using an extensive data set on the Pinaceae, Lambeth (1980) determined that selection for height could take place at one-fifth the rotation age based on

correlations estimated by a regression equation. If this relationship holds, additional studies to determine age-age correlations may not be needed for the species studied. Additionally, examination of the data used by Lambeth revealed a definite pattern when plotting the residuals. Further analysis suggests that individual regression equations for each selection age may be more accurate in predicting these correlations.

Traits with low age-age correlations, which are usually growth traits, present somewhat of a problem. Early selection can still provide better gain per year than later selection, but more good genotypes are left behind and poor ones included because of the low correlations. Better methods are now under study to remedy this situation. One method, based on analysis of genetic components of variation over time (Namkoong et al. 1972; Namkoong and Conkle 1976; Franklin 1979) suggests using methods to accelerate growth of trees to reduce the juvenile period of growth, and hasten the period of maximum genetic variation between trees and families (Franklin 1979). At this stage, selections should be more reliable.

Another method, which could greatly reduce evaluation periods for growth traits, utilizes electrophoresis to determine heterozygosity levels in trees (Mitton et al. 1981). Growth rate variables have been shown to be positively correlated with heterozygosity levels in some forest tree species. This seems logical because of the need for trees to have a diverse genetic background to be able to adapt to changing environments over their long generation interval. Because

electrophoresis can be used to delimit heterozygosity in the seeds of conifers, selection could conceivably take place at this stage. This method obviously needs and deserves further study.

One additional comment to be made concerns short rotation intensive culture forestry. The shorter rotations intrinsically provide for shorter evaluation periods. For a species such as European black alder, rotations of 4-10 years are projected for the production of pulp or biomass for energy. Many benefits to early selection surface when rotations are this short. Selection at one-half the rotation age in this case provides for a short evaluation period. The uniform environment and close spacings projected for use in SRIC can increase selection intensities and heritabilities thus increasing gain. The trees that have the initial spurt of growth, but slow down over longer rotations now may be the desirable ones instead of being the ones to lower age-age correlations. The relationship between early growth and coppice regeneration will have to be studied to determine if early selection will influence coppice growth.

Reducing evaluation periods to 2 to 5 years may create problems with breeding because many tree species do not flower this early. European black alder provides an exception by flowering at 2 years in some cases. Therfore, this species provides an excellent opportunity to try very early selection and breeding for short rotations. Additional work now needed in the newer, better-designed provenance tests and anticipated progeny tests to determine genetic correlations and

heritabilities. With rapid turnover of breeding generations, the incremental gain may be small, but, in the long run, significant advances are likely.

LITERATURE CITED

Allen, P. J. 1978. Genotypic and phenotypic correlations of wood and tree characteristics. Pp. 184-196 in D. G. Nikles, J. Burles, and R. D. Barnes, eds. Proceedings of a joint workshop on Progress and Problems of Genetic Improvement of Tropical Forest Trees. Brisbane, Queensland, Australia, April 4-7, 1977. Dept. of Forestry, Commonwealth Forestry Inst., U. of Oxford, Great Britain.

Balodis, V. 1966. Co-ordinate systems based on the age of growth rings and internodes in trees. J. Inst. Wood Sci. 16:35-42.

Bannan, M. W. 1967. Anticlinal divisions and cell length in conifer cambiums. For. Prod. J. 17(6):63-69.

Bendtsen, B. A. 1978. Properties of wood from improved and intensively managed trees. For. Prod. J. 28(10):61-72.

Boyce, S. G. and M. Kaeiser. 1960. Small increment cores can be use for sampling cottonwood fibers. J. For. 58(6):484-485.

Brazier, J. D. and R. S. Howell. 1979. The use of breast-height core for estimating selected whole tree properties of sitka spruce. Forestry 52(2):177-185.

Bruun, H. H. and S. Sluungaard. 1957. Investigations of porous wood as pulp raw material. 1. Fiber lengths of the species Alnus glutinosa (L.) Gaertn., Alnus incana (L.) Moench, Betula verrucosa Ehrn., and Populus tremula (L.). Papper och Tra 39(11):521-525.

Clausen, K. E. 1982. Age-age correlations in black walnut and white ash. Pp. 113-117 in B. A. Thielges, ed. Proceedings of the Seventh North American Forest Biology Workshop, "Physiology and Genetics of Intensive Culture", July 26-28, 1982. U. of Kentucky, Lexington, KY.

Core, H. A., W. W. Moschler, and C. Chang. 1978. A note on prediction of wood properties in yellow-poplar. Wood and Fiber 9(4):258-261.

Crist, J. B. 1983. Synopsis of utilization research of SRIC raw materials. Pp. 115-118 in Intensive Plantation Culture: 12 years research. U. S. D. A. Forest Service Gen. Tech. Rep. NC-91. North Central Forest Exp. Stn., St. Paul, MN.

DeBell, D. S. and M. A. Radwin. 1979. Growth and nitrogen relations of coppiced black cottonwood and red alder in pure and mixed plantations. Bot. Gaz. 140(Suppl.):S97-S101.

Dickman, D. I. 1975. Plant materials appropriate for intensive culture of wood-fiber in the North Central region. Iowa State J. Res. 49(3):281-286.

Dietrichson, J. 1964. The selection problem and growth-rhythm. Silvae Genetica 13(6):178-184.

Einspahr, D. W. 1976. The influence of short-rotation forestry on pulp and paper quality. II. Short-rotation hardwoods. TAPPI 59(11):63-66.

Einspahr, D. W., J. P. van Buijtenen, and E. F. Thor. 1962. Wood and pulp properties determined from slash pine increment core and whole tree measurments. Silvae Genetica 11(3):68-77.

Falconer, D. S. 1960. Introduction to Quantitive Genetics. The Ronald Press Co., New York. 363pp.

Franklin, E. C. 1977. Juvenile-mature correlations. Pp. 205-212 in D. G. Nikles, J. Burley, and R. D. Barnes, eds. Proceedings of a joint workshop on Progress and Problems of Genetic Improvement of Tropical Forest Trees. Brisbane, Queensland, Australia, April 4-7, 1977. Dept. of Forestry, Commonwealth Forestry Inst., U. of Oxford, Great Britain.

Franklin, E. C. 1979. Model relating levels of genetic variance to stand development of four North American conifers. Silvae Genetica 28(5/6):207-212.

Funk, D. T. 1965. Silvics of European alder. U. S. D. A. Forest Service Central States For. Exp. Stn. Columbus, OH. 21pp.

Funk, D. T. 1973. Growth and development of alder plantings of Ohio strip-mine banks. Pp. 483-491 in R. J. Hutnick and G. Davis, ed. Ecology and Reclamation of Devastated Land. Vol. 1. Gordon and Breach, New York.

Funk, D. T. 1979. Alnus glutinosa provenance trials on Ohio strip mines: sixteen-year results. Pp. 28-32 in R. P. Guries, ed. Proceedings of the First North Central Tree Improvement Conference, Madison, WI, Aug. 21-23, 1979. U. of Wisconsin, Madison, WI.

Geyer, W. A. 1981. Growth, yield and woody biomass characteristics of seven short-rotation hardwoods. Wood Sci. 13(4):209-215.

Giertych, M. 1974. Inadequacy of early tests for growth characteristics as evidenced by a 59-year old experiment. Pp. 237-242 in Proceedings Joint IUFRO Meeting, Stockholm, 1974. Dept. of Forest Genetics, The Royal College of Forestry, Stockholm, Sweden.

Gordon, J. C. and J. O. Dawson. 1979. Potential uses of nitrogen-fixing trees and shrubs in commercial forestry. Bot. Gaz. 140(Suppl.):S88-S90.

Hall, R. B. and C. A. Maynard. 1979. Considerations in the genetic improvement of alder. Pp. 322-344 in J. C. Gordon, C. T. Wheeler, and D. A. Perry, eds. Proceedings of a Workshop, "Symbiotic Nitrogen Fixation in the Management of Temperate Forests," April 2-5,1979. Oregon State University, Corvallis, Oregon.

Hall, R. B., G. A. Miller, T. L. Robison, and O. U. Onokpise. 1983. Developing Alnus for use in intensive culture. Pp. 35-45 in Intensive Plantation Culture:12 Years Research. U. S. D. A. Forest Service, North Central For. Exp. Stn., Gen. Tech. Rep. NC-91. North Central For. Exp. Stn., St. Paul, MN.

Harrington, C. A., D. S. DeBell, and R. F. Strand. 1979. An experiment in biomass production: Results from three consecutive harvests of cottonwood and alder. Pp. 363-366 in Proc. Solar 79 Northwest Symposium, Seattle, WA.

Jett, J. B. and B. J. Zobel. 1975. Wood and pulping properties of young hardwoods. TAPPI 58(1):92-96.

Kellison, R. C. and G. White. 1979. Black alder performance in the Southeast. Pp. 345-355 in J. C. Gordon, C. T. Wheeler, and D. A. Perry, eds. Proceedings of a Workshop, "Symbiotic Nitrogen Fixation in the Management of Temperate Forests," April 2-5, 1979. Oregon State University, Corvallis, Oregon.

Kellogg, R. M. 1982. Coming to grips with wood quality. Forestry Chron. 58(6):254-257.

Kung, F. H. 1975. Development and use of juvenile-mature correlations in a black walnut tree improvement program. Pp. 243-249 in Proceedings of the 12th Southern Forest Tree Improvement Conference, June 12-13, 1973. Louisiana State University, Division of Continuing Education, Baton Rouge, LA.

Lambeth, C. C. 1980. Juvenile-mature correlations in Pinaceae and implications for early selection. Forest Sci. 26(4):571-580.

Larson, P. R. 1969. Wood formation and the concept of wood quality. Yale Univ. School of Forestry Bulletin No. 74. Yale Univ., New Haven, CN. 54pp.

Lester, D. T. and G. R. Barr. 1966. Shoot elongation in provenance and progeny tests of red pine. Silvae Genetica 15(1):1-6.

McKeand, S., W. F. Beineke, and M. N. Todhunter. 1979. Selection age for black walnut progeny tests. Pp. 68-73 in R. P. Guries, ed. Proceedings of the First North Central Tree Improvement Conference, Madison, WI, August 21-23, 1979. U. of Wisconsin, Madison, WI.

Miller, G. A. 1983. Variation in growth, nitrogen fixation, and assimilate allocation among selected Alnus glutinosa (L.) Gaertn. clones. Ph. D. Dissertation. Iowa State University, Ames, IA. 117 pp.

Mitchell, H. L. 1958. Wood quality evaluation from increment cores. TAPPI 41(4):150-156.

Mitton, J. B., P. Knowles, K. B. Sturgeon, Y. B. Linhart, and M. Davis. 1981. Associations between heterozygosity and growth rate variables in three western forest trees. Pp. 27-34 in M. T. Conkle, ed. Proceedings of the Symposium on Isozymes of North American Forest Trees and Forest Insects. Berkeley, CA., July 27, 1979. Pacific Southwest Forest and Range Exp. Stn., Berkeley, CA.

Mohn, C. A. and W. K. Randall. 1971. Inheritance and correlation of growth characters in Populus deltoides. Silvae Genetica 20(5/6):182-184.

Mohrdiek, O. 1979. Juvenile-mature and trait correlations in some aspen and poplar trials. Silvae Genetica 28(2/3):107-111.

Morin, M. J. 1974. NSSC pulping of young European black alder (Alnus glutinosa L. Gaertn.) TAPPI 57(6):133-135.

Namkoong, G. and M. T. Conkle. 1976. Time trends in genetic control of height growth in ponderosa pine. Forest Sci. 22(1):2-12.

Namkoong, G., A. C. Barefoot, and R. G. Hitchings. 1969. Evaluating control of wood quality through breeding. TAPPI 52(10):1935-1938.

Namkoong, G, R. A. Ursanis, and R. R. Silen. 1972. Age related variation in genetic control of height growth in Douglas-fir. Theor. Applied Gen. 42(4):151-159.

Nanson, A. 1967. Modele theorique pour l'etude des tests precoces. (Theoretical model for studying juvenile tests). Biometrie Praximetrie 8(2):84-107. (English summary).

Nanson, A. 1968. Le valeur des tests precoces dans la selection des arbres forestiers en particulier au point de vue de la croissance. Disser. Doct. Gembloux Sta. Rech. Eaux et For., Groenendall-Hoeillart, H. S. No. 38. 242pp.

Nanson, A. 1970. Juvenile and correlated trait selection and its effect on selection programs. Pp. 17-26 in Papers presented at the second meeting of the working group on quantitative genetics, Section 22, IUFRO, Raleigh, NC, August 18-19, 1969. Southern Forest Exp. Stn., New Orleans, LA.

Nanson, A. 1974. Some problems of application of quantitative genetics to forest tree breeding. Pp. 1-15 in Proceedings Joint IUFRO Meeting, Stockholm, 1974. Dept. of Forest Genetics, The Royal College of Forestry, Stockholm, Sweden.

Nanson, A. 1976. Juvenile-mature relationships mainly in provenance and progeny tests. Pp. 99-119 in Proceedings of the IUFRO joint meeting of genetic working parties on advanced generation breeding. Bordeaux, June 14-18, 1976. INRA, Laboratoire d'Amelioration des Coniferes, 33610 Cestas, France.

Panshin, A. J. and C. DeZeeuw. 1980. Textbook of Wood Technology. Fourth Edition. McGraw-Hill Book Company. New York.

Philipson, W. R. and B. G. Butterfield. 1967. A theory on the causes of size variation in wood elements. Phytomorphology 17(1/4):155-159.

Plass, W. T. 1977. Growth and survival of hardwoods and pine interplanted with European alder. U. S. D. A. Forest Service Res. Pap. NE-376. Northeastern Forest Exp. Stn., Upper Darby, PA. 10 pp.

Rehfeldt, G. E. 1983. Genetic variability within Douglas-fir populations: implications for tree improvement. Silvae Genetica 32(1/2):9-14.

Resch, H. 1979. Industrial uses and utilization potential for red alder. Pp. 388-402 in J. C. Gordon, C. T. Wheeler, and D. A. Perry, eds. Proceedings of a Workshop, "Symbiotic Nitrogen Fixation in the Management of Temperate Forests." April 2-5,1979. Oregon State University, Corvallis, Oregon.

Richardson, S. D. 1961. A biological basis for sampling in studies of wood properties. TAPPI 44(3):170-173.

Robison, T. L. 1984. Age-age correlations, trait correlations, and wood property variation for an Alnus glutinosa (L.) Gaertn. provenance study. Ph. D. Dissertation. Iowa State University, Ames, Iowa. 81pp.

Robison, T. L. and R. B. Hall. 1981. Approaches to European alder improvement. Pp. 65-77 in R. P. Guries, ed. Proceedings of the Second North Central Tree Improvement Conference, Lincoln, NE.

Robison, T. L., C. A. Maynard, J. Thomas, and R. B. Hall. 1979. A germplasm collection and evaluation program for Alnus glutinosa . Pp. 73-85 in K. Steiner (ed.), Proceedings of the 26th Northeastern Forest Tree Improvement Conference, University Park, PA. July 25-26, 1978. Northeastern Forest Exp. Stn., Durham, NH.

Schmidt, W. 1963. Early tests. FAO/FORGEN 63 2a/10 in Proceedings World Consultation of Forest Genetics and Tree Improvement, Vol. 1. Stockholm, Sweden. August 23-30, 1963. Rome:FAO.

Schmidt-Vogt, H. 1969. Growth and root development in Alnus glutinosa of different provenances. Pp. 725-731 in Proc. Second World Consultation on Forest Tree Breeding. Washington, D. C. FO-FTB:69-6/12.

Smith, D. M. 1954. Maximum moisture content method for determining specific gravity of small wood samples. U. S. D. A. Forest Service FPL Report No. 2014. Forest Products Lab., Madison, WI. 3pp.

Smith, W. J. 1967. The heritability of fiber characteristics and its application to wood quality improvement in forest trees. Silvae Genetica 16(2):41-51.

Squillace, A. E. and C. R. Gansel. 1974. Juvenile-mature correlations in slash pine. Forest Sci. 20(3):225-229.

Steinhoff, R. J. 1974. Juvenile-mature correlatins in ponderosa and western white pines. Pp. 243-250 in Proceedings Joint IUFRO Meeting, Stockholm, 1974. Dept. of Forest Genetics, The Royal College of Forestry, Stockholm, Sweden.

Sziklai, O. 1974. Juvenile-mature correlation. Pp. 217-235 in Proceedings Joint IUFRO Meeting, Stockholm, 1974. Dept. of Forest Genetics, The Royal College of Forestry, Stockholm, Sweden.

Verweij, A. A. 1977. [Research on provenances and progenies of alder (Alnus glutinosa, Alnus incana, and Alnus cordata)]. Rijksinstituut voor onderzoek in de bosen landschapsboow "De Dorschkamp," Wageningen. Uitvoerig verslag. 15(1):1-23. (Dutch with English summary and captions).

Vurdu, H. and D. W. Bensend. 1979. Specific gravity and fiber length in European black alder roots, branches, and stems. Wood Sci. 12(2):103-105.

Wahlgren, H. E. and D. L. Fassnacht. 1959. Estimating tree sppecific gravity from a sinngle increment core. U. S. D. A. Forest Products Lab. Rep., Tech. Publ. No. 2146. Forest Products Lab., Madison, WI. 9pp.

Wakeley, P. C. 1971. Relation of thirtieth-year to earlier dimensions of Southern pines. Forest Sci. 17(2):200-209.

Wilcox, M. D. 1977. Some problems in selection to improve wood properties. Pp. 213-225 in D. G. Nikles, J. Burley, and R. D. Barnes, eds. Proceedings of a joint workshop on Progress and Problems of Genetic Improvement of Tropical Forest Trees. Brisbane, Queensland, Australia, April 4-7, 1977. Dept. of Forestry, Commonwealth Forestry Inst., U. of Oxford, Great Britain.

Wilkinson, R. C. 1974. Realized and estimated efficiency of early selection in hybrid poplar clonal tests. Pp. 26-32 in P. W. Garrett, ed. Proceedings of the 21st Northeastern Forest Tree Improvement Conference. Fredericton, New Brunswick. August 27-30, 1973.

Wittmer, R. F., and M. J. Immel. 1977. A comparison of five tree species for intensive fiber production. For. Ecol. Manage. 1:249-254.

Zavitkovski, J., E. A. Hansen, and H. A. McNeel. 1979. Nitrogen-fixinng species in short rotation systems for fiber and energy production. Pp. 388-402 in J. C. Gordon, C. T. Wheeler, and D. A. Perry, eds. Proceedings of a Workshop, "Symbiotic Nitrogen Fixation in the Management of Temperate Forests." April 2-5, 1979. Oregon State University, Corvallis, Oregon.

Zobel, B. 1981. Wood quality from fast-grown plantations. TAPPI 64(1):71-74.

Zobel, B. and R. C. Kellison. 1978. The rate of growth syndrome. Silvae Genetica 27(3/4):123-124.

Zobel, B., C. Webb, and F. Henson. 1959. Core or juvenile wood of loblolly and slash pine trees. TAPPI 42(5):345-356.

Zobel, B., F. Henson, and C. Webb. 1960. Estimation of certain wood properties of loblolly and slash pine trees from breast-height sampling. Forest Sci. 6(2):155-162.

Zobel, B., E. Campinhos, Jr., and Y. Ikemori. 1983. Selection and breeding for desirable wood. TAPPI 66(1):70-74.

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